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THE UNIVERSITY OF ALBERTA

DDE AND EGGSHELL THICKNESS IN ALBERTA COMMON TERNS

BY

BRUCE CORNEILLE SWITZER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

IN

ENVIRONMENTAL STUDIES

DEPARTMENT OF FOOD SCIENCE

EDMONTON, ALBERTA

SPRING 1989

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled DDE AND EGGSHELL THICKNESS IN ALBERTA COMMON TERNS submitted by BRUCE CORNEILLE SWITZER in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY IN ENVIRONMENTAL STUDIES.

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Date: 10 April 1981

DEDICATION

For Michael Curcio,
a good and honorable man who was my friend.
I have not forgotten.

ABSTRACT

A colony of common terns (*Sterna hirundo*) at Chip Lake, Alberta, Canada, containing high residue levels of DDE was studied from 1969 to 1972 to determine if DDE influenced reproductive success through eggshell thinning. It is likely that the DDE was accumulated mainly on the west coast of California, Central America, and northern South America. The levels of DDE as reflected in the tern eggs significantly declined each year of the study and this was a reflection of decreasing DDT use. Eggshell thickness was unrelated to DDE over the time of the study, within years, within the clutch sequence, or to fracturing of eggshells. The number of highly contaminated eggs declined significantly each year, but the number of thinner-shelled eggs remained constant. The relationship between DDE and eggshell thickness is most probably a function of natural extrinsic and intrinsic factors which are coincidental with the levels of DDE observed.

The breeding population varied without trend over the term of the study and reproductive success was influenced by factors normal for the species. Reproductive success was probably negatively influenced by investigation, but otherwise it would have been adequate for population maintenance for two of the four years. The most important natural factors influencing reproductive success were displacement by California gulls (*Laurus californicus*) and ring-billed gulls (*L. delawarensis*) and flooding.

A review of the literature within the context of the findings of this study suggests that the DDE/eggshell thinning hypothesis is invalid insofar as many species of birds are concerned. Several studies suffer from inappropriate statistical interpretation; in others, conclusions are drawn which are paradoxical or contradictory. Many other factors which may more readily explain population declines or increases in species purportedly affected by DDE have been ignored.

It has been concluded that DDE at the levels observed in this population did not influence reproductive success.

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Mr. Stan Calder prepared the manuscript and Mr. Ernie Toth prepared the drawings. They both suffered through several revisions and I thank them.

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I. INTRODUCTION

Shortly after the introduction and widespread use of DDT as an insecticide, concern mounted over its environmental side effects on wildlife. Originally general in scope, this concern soon focused upon the effects of DDT on reproduction in predatory birds. Following a 1965 conference that devoted attention to the peregrine falcon (Falco peregrinus), studies of this species and of other avian predators were initiated. Because most of these studies, however, were short term and of a survey nature, it seemed important at the conception stage of my study to undertake a long-term intensive investigation of a single population that would test the hypothesis that failure of reproduction in predatory birds was caused by DDT. At Chip Lake, Alberta, a population of common terns (Sterna hirundo) which contained high levels of DDE was discovered in 1968; and this population was selected for a four-year intensive study.

II. DDT

HISTORY

In 1939, Paul Muller of Switzerland discovered the insecticide properties of DDT, for which he was awarded the 1948 Nobel Prize in Medicine. Employed by the Geigy Company, which patented DDT in 1942, Muller found a practical application for the chemical first formulated in the laboratory in 1874 (Beatty, 1973).

DDT derives its colloquial name from its earlier chemical designation, dichlorodiphenyl trichloroethane. Currently, however, the chemical nomenclature for p,p' DDT is 1,1,1-trichloro-2,2-bis (p-chlorophenyl) ethane.* By 1969, DDT was only one of 900 registered chemicals of synthetic and natural origin (Murphy, 1975) used to control a taxonomically wide range of organisms that man considers harmful or interruptive. Most efforts in chemical pest control, however, have been directed at insects. In fact, more of the insecticide DDT had been used up to the time of this study than any other single insecticide (Hartley and West, 1969).

The search for effective means of insect control has a lengthy history, but this was conducted mostly in vain until attention was drawn to synthetic compounds of organic origin. To be sure, some of the most toxic chemicals known are of natural origin: strychnine, curare, and snake venom; and some naturally occurring chemicals are toxic to insects and have been used as insecticides. For example, nicotine, rotenone, and pyrethrum all have insecticidal properties; pyrethrum was used in the Middle and Far East to control body lice and was introduced in Europe around 1851 for this specific purpose (Hartley and West, 1969). Most naturally occurring organic compounds with insecticidal properties, however, share two qualities that make them unsuitable for large-scale practical application: rapid degradation and expense or complication of extraction and refinement (Mellanby, 1967).

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* See Appendix 1 for chemical names of DDT and metabolites, and Appendix 2 for chemical structural formulae.

Although cultural and biological insect control was promoted before introduction of synthetic chemicals, this approach did not find social or political acceptance; the answer to insect control seemed, then, to lie in the use of synthetic compounds, the first of which were inorganic. In 1867 Paris green, a compound of acetate and arsenite of copper, was used in the United States against the Colorado potato beetle (Dunlap, 1981); and compounds containing arsenic, fluorine, and cyanide were widely used for nearly a century. These inorganic compounds, however, are not particularly effective and are generally highly toxic to most vertebrates (Mellanby, 1967). When the first synthetic organic insecticide—DDT—was introduced in 1942, its instant success immediately made redundant the use of the earlier insecticides. Although many other organic insecticides have been synthesized since, the remainder of the discussion deals primarily with DDT and its metabolites.

2

DDT was first used in Naples, Italy, in 1943, by the Allied armies in their successful efforts to arrest a potential typhus epidemic, the first in history (Hartley and West, 1969). Although pyrethrum was used with DDT in this program, its contribution was downplayed (Dunlap, 1981). Soon after, DDT programs to eradicate typhus and other insect-borne diseases were conducted throughout the world in areas where such diseases were endemic (Mellanby, 1967). The concentrated and widespread program to eradicate malaria best illustrates the medical impact of DDT. Conducted by the World Health Organization (WHO), this program achieved remarkable success; Russell (1968) estimated that more than 960 million people who were subject to malaria endemicity became virtually free of the disease. In India, for example, Pal (1962) attributed 750,000 deaths annually to malaria prior to the use of DDT. In view of the fact that only about one in one hundred is fatally infected, this number does not consider the much greater consequence of severely debilitated survivors. Unable to effectively contribute, these individuals burden society; hence incapacitation from malaria, as from other debilitating diseases less well-known such as onchocerciasis, has had a greater social impact than mortality (I.D.R.C., 1972).

Initially, DDT was unavailable for non-medical use because of expense and limited availability as well as the imperatives of World War II. A few years following its introduction for disease control, production of DDT was increased and its cost was sufficiently reduced by 1948 to allow its practical agricultural use (Gunn, 1972a). It achieved instant success against many plant pests and helped increase food production in many areas where famine was common

(Ling et al., 1972). The uses of DDT increased throughout the world until the late 1950's and early 1960's. In the United States, the peak year of DDT use was 1958, when 78 million pounds were used (Dunlap, 1981). The use of DDT in the United States steadily decreased between 1958 and 1970, when less than 12 million pounds were used (Consolidated DDT Hearings, 1972a). In fact, DDT production in the United States declined 50% between 1969 and 1970 (Edwards, 1973).

In North America, DDT was used initially in attempts to control any insect pest. It was used in the agriculture and fiber industries on a variety of crops including tobacco, cotton, and soybeans; in forestry for gypsy moth and spruce budworm control; in urban areas for control of the elm bark beetle, which transmits dutch elm disease; in public health by application to marshes and wetlands for control of dipteran disease vectors; in and around homes as a house and garden spray; and in and around recreational areas for control of mosquitoes and other dipteran pests. In fact, DDT was used against anything which swam, crawled, or flew and remotely resembled an insect. It was even used in an attempt to control polio (Dunlap, 1981).

Following the peak years of its use in the United States, DDT application steadily declined for such purely practical reasons as its inability to control certain problems such as the transmission of dutch elm disease and for such environmental reasons as its side effects on salmon and trout fry (Gunn, 1972a). By 1969, with mounting public concern over environmental problems, the Environmental Defense Fund (E.D.F.) found support to file a petition before the United States Department of Agriculture (U.S.D.A.) to suspend and ultimately cancel all uses of DDT that were registered under the Federal Insecticide, Fungicide, and Rodenticide Act.

Although the Secretary of the U.S.D.A. did not comply, the court ruled that the issue of DDT safety warranted instigation of the public hearing which began on August 17, 1971. Following this hearing, the Hearing Examiner ruled that uses of DDT which were considered necessary by the U.S.D.A. be continued. The Administrator of the Environmental Protection Agency (E.P.A.), however, overruled this decision, which the cotton industry in turn appealed to the District of Columbia Circuit of the United States Court of Appeal. On December 13, 1972, this court ruled that the decision of the E.P.A. was to be upheld. During the court proceedings, all registrations of DDT were suspended in the United States and, in accordance with the Appelate Court's ruling, all non-medical uses of DDT were banned (Dunlap, 1981). This action, although not accompanied by lengthy judicial proceedings, had been preceded by partial or complete bans in Canada; although it still may be used in medical emergencies, it is essentially prohibited in Canada and the United States.

CHEMISTRY

Zeidler's preparation of DDT through condensation of chloral (Cl_3C_2HO) and monochlorobenzene (ClC_6H_5) agitated with strong sulfuric acid (H_2SO_4) is still the basis of commercial preparation. The heat of this reaction rises to about 60°C at completion and, after cooling, the mixture is poured into excess water where the DDT crystallizes and is filtered. Only about 70-75% of the chloral condenses on the positions para to the chlorine substituents in the benzene ring. In addition to the p,p' compound, o,p' is produced together with traces of o,o' and of oily byproducts and in some preparations of small amounts of other DDT-related compounds (Azevedo et al., 1965). This commercial mixture is referred to as technical grade DDT.

The melting point of pure p,p' DDT is 108°C, and the melting point of the technical grade is somewhat lower (Hartley and West, 1969). Pure p,p' DDT has an extremely low vapor pressure (1.5 X 10^{-7} mm at 20°C) which enables DDT to persist on surfaces for lengthy periods (O'Brien, 1967). DDT resists photodegradation, another quality important in regard to persistence. O'Brien (1967) states that the most accurate estimates of the water solubility of DDT are in the order of 1.2 ppb (3.4 X 10^{-10} M at 25°C). However, values as low as 0.2 ppb (Brown, 1951) and as high as 40 ppb (Ling et al., 1972) have been recorded. Superimposed on this excessively low water solubility is extreme apolarity, with an oil-water partition coefficient of 923:1 for olive oil:water (O'Brien, 1967). The only facile reaction that DDT undergoes is to lose hydrogen chloride at the aliphatic center of the molecule under alkaline conditions yielding DDE (Brooks, 1974). Accordingly, a picture emerges of a chemical which persists on surfaces, which is virtually water insoluble, which does not readily vaporize or co-distill with water under normal environmental conditions, and which is lipophilic.

Gas liquid chromatography with electron capture detection systems was the most sensitive and accurate analytical system available for analysis of chlorinated hydrocarbon insecticides. This system, however, is sensitive to all halogenated hydrocarbons and will produce a response to any electronegative compound.

In 1968, Risebrough (1968) and Reynolds (1969) reported that the presence in the environment of polychlorinated biphenyls (PCB's) presented a problem in accurately indentifying and quantifying DDT and its metabolites. PCB's are a family of chlorine bearing compounds that were used for 45 years in a variety of industries, especially the plastics industry (Edwards, 1973). They are marketed under the trade name Arochlor. Each of these mixtures contains a number of chlorinated biphenyl isomers with an overall range of chlorine varying from one to ten chlorine molecules per isomer (E.P.A., 1976).

They are among the more stable organic compounds, and they are structurally very similar to DDT. Accordingly, they exhibit similar environmental properties e.g. they are lipophilic and hydrophobic, are accumulated in lipid tissue, and respond to electron capture detection in a similar fashion to DDT and its metabolites (Edwards, 1973; E.P.A., 1976). It is highly probable that many studies which reported organochlorine insecticides prior to the early 1970's were in fact reporting varying and sometimes large amounts of PCB's as DDT (Edwards, 1973).

I also identified the problem of contamination by PCB's in 1969 (Switzer et al., 1971) and the methods I developed to resolve this problem are described later.

TOXICITY AND MECHANISM OF ACTION

Toxicity may be considered in terms of acute or subacute effects on the individual. Acute toxicity is the gross and relatively rapid response of an individual organism to a toxicant; and unless several individuals thus respond, such toxicity does not generally significantly affect the population. Subacute toxicity resulting from prolonged exposure can cause the death of an individual. However, prolonged exposure may not affect an individual's well-being, but it theoretically could—through alteration of the individual's reproductive function—impact the population to which the individual belongs.

The acute toxicity of DDT is conceptually expressed in terms of lethal dose (LD) or lethal concentration (LC), most often in terms of LD_{50} or LC_{50}, which is the dose or concentration required to induce 50% mortality in an experimental group of animals. The route of administration determines the magnitude of the dose required to achieve LD_{50}, and intravenous introduction is generally most toxic (Metcalfe, 1955). Intraperitoneal and oral introduction are the next most toxic applications; cutaneous or topical application is least toxic. These differences are generally attributed to "barrier effects" of the integument and seem to apply to most organisms tested (O'Brien, 1967). From an environmental point of view, however, only the oral and topical routes are relevant.

DDT has a wide spectrum of acute toxicity among different classes of arthropods and is not uniformly toxic to all species. Spiders and mites are, for instance, less susceptible than most species (Hartley and West, 1969). Honey bees, though they are also relatively insensitive to topical contact with DDT, are quite sensitive to oral ingestion (O'Brien, 1967). The American cockroach and housefly, on the other hand, are very sensitive to topical contact (Metcalfe, 1955). The relative susceptibility of different species to acute toxicity has been termed "physiological selectivity" (Ripper et al., 1951). The relative susceptibility of many species of insect pests is further complicated by their behavior or by the niche they occupy which removes them wholly or partially from contact with an insecticide. This concept has been termed "ecological selectivity" as distinct from the purely experimental concept of physiological selectivity (Ripper et al., 1951). Further complicating ecological selectivity is relative toxicity. A pest may, for example, be sensitive to DDT, but its predators may be even more sensitive. Control of the primary pest population may be followed by a resurgence of the second population that may, because of the relative reduction in natural predators and parasites that do not recover as rapidly, surpass the first in numbers.

Even when great variations in physiological and ecological selectivity are considered, arthropods as a group are the most sensitive invertebrates to DDT (O'Brien, 1967).

Among vertebrates, fish (particularly salmonids) are the most sensitive to acute toxicity of DDT (Brown, 1951; Chichester, 1965). Amphibians and reptiles, though they are generally more sensitive than birds, are somewhat less sensitive than fish; mammals are the least sensitive of vertebrates (Brown, 1951; Chichester, 1965).

Concerning the mechanism of action of the toxicity of DDT, O'Brien (1967) states that "we are far from understanding the mechanism of action of DDT"; Hartley and West (1969) add that "The biochemistry of the action of DDT is still obscure." These statements are repeated by St. Omer (1970) and Brooks (1974) and are apparently still true (Durham, 1987).

The sequence of physiological effects in lethally dosed cockroaches occurs in a time span of approximately 24 hours, where tremor is followed by hyperexcitability, ataxia, paralysis, and finally death. In the housefly, the same events occur but are complete in a few hours; in birds and mammals, similar symptoms of hyperexcitability, ataxia, paralysis, and death have been observed (O'Brien, 1967). In vitro experimental work with many species has shown conclusively that only nervous tissue is sensitive to low concentrations of DDT, and effects are principally upon sensory nerves (Brooks, 1974; Coats, 1982). It is apparent, then, that the mechanism of action of DDT is associated with its effects on sensory nerves, and it is generally concluded that toxicity of DDT is associated with its properties as a neurotoxicant.

METABOLISM

The known and probable pathways of DDT metabolism in various organisms are well-known (Matsumura, 1975).* The five primary end products and their mechanism of metabolism include oxidation to kelthane and DDA, reduction to DBP, dehydrochlorination to DDE, and dechlorination to DDD (O'Brien, 1967; Bailey et al., 1969; Datta and Nelson, 1970; Matsumura, 1975). Of these metabolites, the only ones that exhibit properties of acute toxicity, except for administration of heroic doses, are kelthane and DDD (Ling et al., 1972).

It is established that the major metabolites of DDT in homeotherms are DDA—which is excreted in the feces and urine—and DDE—which is stored in depot fat—(Bailey et al., 1969), although this simplified view is complicated by species variation. Nevertheless, this general duality of conversion occurs in many mammals and particularly in most species of birds (Stickel et al., 1966; Bailey et al., 1969).

Research shows that in homeotherms the hepatic microsomal system is inducible; presumably metabolism of the apolar compounds occurs here (Abou-Donia and Menzel, 1968; Peakall, 1970a, 1970b). Water-soluble polar compounds are metabolized in the kidney (Ottoboni et al., 1968; Datta and Nelson, 1970).

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* See Appendix 2 for metabolic pathways.

PROBLEMS OF USE

Resistance

Owing to the increased use of DDT following World War II, DDT-resistant strains of insects appeared, in some instances as early as 1948; by 1968, 200 or more insect pests were reportedly resistant to one or more insecticide(s) (Ling et al., 1972). This continually increasing level of pesticide resistance, in the absence of effective and economically alternative compounds, led usually to increased rates and amounts of DDT application. The problem was recognized as early as 1950, and much effort was expended in search of alternative insecticides.

In the field, resistance normally appears as the progressive inability to achieve control through a fixed application rate; resistance may be defined as "the development of an ability in a strain of insects to tolerate doses of toxicants which would prove lethal to the majority of individuals in a normal population of the same species" (O'Brien, 1967). It is generally concluded that this ability is attributable to the presence of a DDT dehydrochlorinase in resistance species (O'Brien, 1967; Agosin et al., 1969; Hodgson, 1987).

Transport

DDT, because of its persistence, could logically be expected to move from sites of application; increased application would result in increased amounts being transported from the intended target area. In fact, DDT appeared in areas remote from the nearest site of application and several mechanisms were proposed to account for this mobility. These include wind drift during application (Antommaria et al., 1965); volatilization (Benvenue et al., 1972); evaporation (Abbot et al., 1966); and harvest of organic material, run-off, and animal ingestion (Woodwell et al., 1971).

During and following application, molecules of DDT can attach themselves to dust particles and travel to areas removed from sites of application. They are then scrubbed out of the atmosphere by precipitation (Woodwell et al., 1971). As illustration of this, Risebrough et al. (1968) report that about 600 kg of DDT, its metabolites, and dieldrin attached to dust particles were carried by equatorial easterly winds and deposited annually in the Atlantic Ocean with rainwater. Samples of Pacific air, on the other hand, showed no detectable residues (ibid.). In Great Britain, Tarrant and Tatton (1968) recorded average amounts of 46 ppt of DDT plus metabolites in rainwater; and Wheatly and Hardman (1965) found average rainfall concentrations of 3 ppt. In the United States, Cohen and Pinkerton (1966) found 150 ppt in rainfall in Ohio, and Benvenue et al. (1972) found 3-4 ppt in Hawaii. DDT has also been reported in remote parts of the world where it presumably arrived via wind-blown particles (George and Frear, 1966; Peterle, 1969).

It is clear, then, that small amounts of DDT attached to dust particles can be carried to extremely remote parts of the world and deposited with precipitation. It is also clear that the highest levels of DDT in rainwater are close to sites of application and are, in fact, often 1,000 times greater than levels in areas removed from DDT use (Risebrough et al., 1968). Even in an area as small as Hawaii, atmospheric residue levels correlate with areas of use and non-use (Benvenue et al., 1972).

Woodwell et al. (1971) suggest that vaporization is an important transport mechanism and that DDT and its metabolites can be lost from soil by volatilization. Robinson (1973), however, concludes on the basis of a review of the literature respecting this matter, that chlorinated hydrocarbons in the atmosphere are trapped as particulate matter and are in this form and not in the form of vapor.

Other modes of movement of DDT from the site of application (such as through co-distillation with water or crop or timber harvest) are not major sources of DDT transportation (Acree et al., 1963; Guenzi and Beard, 1967; Yule et al., 1972) nor is movement by livestock a significant avenue of transport (Woodwell et al., 1971).

DDT finds its way into surface waters mainly through soil erosion and drift during application (Ling et al., 1972), and its presence in soil is primarily a direct result of local application—even though DDT is found in some soil samples well removed from any area of use. Nevertheless, the chemical properties of DDT result in its absorption by soil particles; the presence of DDT in fresh water is largely due to soil erosion (Ling et al., 1972). Without exception the amount of DDT in soils is a function of the amounts used, and the amounts present in areas of application greatly exceed those present in areas of no application (Woodwell et al., 1971; Ling et al., 1972). Drainage systems near agricultural areas would, therefore, be expected to contain the highest levels of DDT. In support of this observation, the highest aquatic concentration of DDT and its metabolites (0.72 ppb) in 1966 in the United States was in the Mississippi River Delta, which drained the area of greatest DDT use during that year (U.S.D.A., 1966). Even during years of greatest use, however, American rivers near sites of heavy application contained less than 10 ppt of DDT and metabolites (Weaver et al., 1965).

It may be concluded that the major sources of global dispersal of DDT result from aerial particulate matter and particulate matter in run-off and that environmental residues are significantly greater near and on areas of direct application—although DDT is ubiquitous in the biosphere.

Persistence

Following application, DDT and its related compounds retain their structural integrity for varying periods of time. Wooden stakes impregnated with DDT, for example, maintain their insecticidal properties for as long as ten years (Ling et al., 1972). But despite this retention of chemical integrity, sweeping generalizations concerning the persistence of DDT would be erroneous in reference to most environmental circumstances.

Menzies (1969) shows that, in certain anaerobic soils, the half-life of DDT is only 4 weeks; Guenzi and Beard (1967) show that in some anaerobic soils 99% of added DDT was broken down in 12 weeks and that in rich aerobic soil 80% of added DDE was lost in 3 weeks. Cooke et al. (1982) report that DDT declines rapidly, especially in moist soil and silt. Hill and McCarty

(1967) found that in snow sludge DDD had a half-life of 4 days and that anaerobic conversion of DDT to DDD was "too rapid to classify." Baker and Applegate (1970) show that temperature and ultraviolet light influence degradation of as much as 79% of DDT added to soil in 2 months, and Burge (1971) found that in anaerobic soil conditions 74% of DDT could be metabolized to unknowns in 166 days. Clearly, then, DDT applied to soil is degraded in amounts and in time periods that may be highly variable but which are usually of a few months' duration. Non-metabolic pathways such as seepage into ground water cannot account for the disappearance, since it has been shown in agricultural areas that springs and bore holes 12-45 meters in depth contained no detectable levels of DDT (Agric. Res. Counc. U.K., 1970).

With respect to persistence of DDT in the marine environment, one of the best indications was the oyster monitoring program of the E.P.A. of the United States Government. Over 6,500 oyster samples were taken from 170 stations on the Atlantic, Pacific, and Gulf coasts during the mid-1960's. This study showed that, in estuarian areas where little agriculture was conducted, less than 3% of the oysters contained DDT or its metabolites. Near areas where DDT use in agriculture was intensive, however, all samples showed contamination generally averaging but rarely exceeding 1.0 ppm (Butler, 1973). Moreover, levels in the same estuary were often highly variable, which suggests a fairly rapid decay. The significance of the oyster monitoring program is that the oyster is a filter feeder capable of concentrating DDT and its metabolites by a factor of 75,000 to 100,000 and therefore serves as a good bioassay of marine and estuarian water and particulate matter contamination. Levels of DDT in estuaries near agriculture could then be calculated and were in the order of 1-2 ppt. The program was discontinued because of these low levels. In 1977 it was reinstituted in 87 estuaries, and only 2 sites showed detectable residues of DDE (Butler _et al._, 1978).

ENVIRONMENTAL EFFECTS OF DDT

Research shows that an accumulation in the muscle tissue of salmonids of as little as 5 ppm of DDT, originally taken in through respiration, can be fatal (Ling _et al._, 1972; Gunn, 1972). Salmonid fry are even more sensitive and 1 ppb results in 50% mortality (ibid.). In other economically significant fish, Ling _et al._ (1972) state that some species such as cod are capable of carrying "hundreds of times as much DDT" as salmonids without ill effects.

With respect to birds, the effects of DDT application on songbirds in the immediate areas of application were documented early by Robbins _et al._ (1951) who showed that, of 27 species, three species—red-eyed vireo (_Verio olivaceus_), parula warbler (_Parula americana_), and American redstart (_Setophaga ruticilla_)* were affected by 2 lb/acre applications of DDT. It was not known whether these reductions were caused by toxicity or by depletion of insect prey and consequent emigration of the birds. Stickel _et al._ (1966) studied the effects of DDT spraying on songbirds and concluded that such birds were not affected by levels of less than 3 lb/acre. The use of DDT for tree spraying, particularly in controlling dutch elm disease, led to depletions in robin (Turdus migratorius) populations.

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* Nomenclature of birds is after the A.O.U. (1983).

Earthworms, relatively insensitive to DDT, can accumulate enough DDT to cause mortality among robins which feed on them in sprayed areas (Wurster et al., 1965). American woodcock (Scolopax minor), who consume earthworms, are similarly affected. In this case, the source of chlorinated hydrocarbons was from spruce budworm control programs (Wright, 1965).

The major issue respecting DDT was not, however, concerned with acute toxicity or with widespread effects on all wildlife; it focused, rather, on the subacute chronic effects of DDT—and its principal avian metabolite, DDE—on reproduction in certain avian predators.

The first indication that DDT might be influencing reproductive physiology in birds originated in England following a survey conducted in 1961-1962 by the British Trust for Ornithology of the number, distribution, and food habits of the peregrine falcon. This survey coincided with a decline in the number of breeding peregrine falcons in parts of Great Britain that began around 1956-1957 and continued into 1962-1963 and then increased to near 1956-1957 levels by 1980 (Ratcliffe, 1958, 1967a, 1967b,1980).

Ratcliffe's observations stimulated research both in his own country and in North America, and from this research the theory emerged that DDE was magnified through ascending trophic levels of the ecosystem in amounts sufficient to cause aberrant reproductive physiology in avian apical predators.

It was hypothesized that the primary effect of this accumulation was eggshell thinning, which results in eggshell breakage during incubation.

That the physio-chemical properties of DDT lend themselves to accumulation by individual organisms exposed to low levels of DDT was recognized very early; theoretically any compound which is hydrophobic, persistent, and lipophilic could be expected to funnel its way into the lipid fraction of ecosystems.

There is little doubt that DDT and its metabolites accumulate through ascending trophic levels in short-chain food-webs in or near areas of DDT use, with the robin and woodcock examples as cases in point. With respect to accumulation on an ecosystem scale, examples occurred at Clear Lake, California, where DDD was sprayed for black fly (*Chaborus astictopus*) control (Hunt and Bischoff, 1960). Although the analytical techniques of the time were not sensitive enough to allow analysis of water or phytoplankton, it was clear that DDD was generally magnified through the Clear Lake aquatic ecosystem. Following this study, DDT and metabolite accumulation were reported in the cases of other aquatic ecosystems in the United States: for instance in Big Bear Lake (Hunt and Keith, 1963), in Tule Lake National Wildlife Refuge (Keith *et al.*, 1963), and in Lake Michigan (Hickey *et al.*, 1966). Several other examples are summarized by Rudd (1964). Hickey *et al.* (1966) found that in Lake Michigan the amphipod *Pontoporeia affinis* accumulated about 30 times as much DDT and metabolites as bottom sediments. Fish feeding on P. *affinis* accumulated about 10 times as much, and fish-eating birds accumulated 15-30 times as much DDT as the fish sampled.

Most early studies of aquatic ecosystems showed this same kind of trophic level accumulation. Later research, however, with more sensitive analytical equipment and larger sample sizes, failed in many instances to find such a straight line kind of accumulation from lower to higher trophic levels (Lyman et al., 1968; Jensen et al., 1969; Herman et al., 1969; Hamelink et al., 1971). Matsumura (1975) attributes this to the complexity of processes involved in various ecological systems.

In birds, residue levels found in tissue or eggs in members of the same species are usually highly variable and the distributions virtually always nongausian (Risebrough, 1971; Coulson et al., 1972; Spitzer et al., 1977). An illustration of this variability was the residues (ranging from less than 1 ppm to over 200 ppm wet weight)* in 40 great blue heron (Ardea herodias) eggs from Western Canada. The arithmetic mean in this illustration was 37 ppm with only two observations exceeding it, and only 5 exceeding 20 ppm (Vermeer and Reynolds, 1970). This suggests that assimilation at any given trophic level is influenced by a number of variables and that DDT and its metabolites are not uniformly distributed in lower trophic levels. It also suggests that extrinsic and intrinsic factors differentially influence concentration and excretion of DDT in an individual.

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* Levels of chlorinated hydrocarbons in a sample are reported in three ways: on a wet weight basis, a dry weight basis, or a lipid weight basis. In the case of wet weight analysis, the chlorinated hydrocarbons are analyzed from a sample of the fresh whole tissue. In the case of dry weight analysis, the tissue is completely dried before analysis. In the case of lipid weight analysis, the lipid fraction is extracted prior to analysis of chlorinated hydrocarbon content.

The clearest examples of biomagnification in birds have all occurred in connection with DDT uses over or in water, over forests, or in dutch elm disease control. Woodwell et al. (1971) and Ratcliffe (1972) point out that readily identifiable harm from DDT use invariably occurs in or near the area of use. Many species of birds, however, winter in areas where DDT is being used or was used; although these species breed in relatively uncontaminated areas, they could theoretically return to their breeding areas with residue levels sufficiently high to cause changes in reproductive physiology. Alternatively, prey species could return with residues high enough to affect an otherwise uncontaminated predator population.

Ratcliffe's early observations were largely restricted to a population decline in peregrine falcons and to a measurement of pre- and post-pesticide era eggshells of the same species. In regard to the population decline in peregrine falcons, he showed an approximate 16% decrease in an eggshell index (Ratcliffe's Index = weight of eggshell/length x width) which was correlated with the onset of DDT use in England. DDT, by causing thin eggshells, was therefore implicated in the population decline. In North America, DDT was also implicated in the decline of the peregrine falcon in the Eastern United States on the basis of a reduction in thickness of eggshells when post-DDT era eggshells were compared to pre-DDT era eggshells (Hickey and Anderson, 1968). The tasks of gathering quantitative field data and of conducting laboratory work with the peregrine falcon are difficult because of the behavior and ecology of this species; hence, by way of compensation, studies of other species were also conducted in the laboratory and the field.

In addition to the peregrine falcon (Cade *et al.*, 1968, 1971), field studies of several other species of predators were conducted: with the osprey (*Pandion haliaetus*) (Ames, 1966), with the herring gull (*Larus argentatus*) (Hickey and Anderson, 1968), with the great blue heron (Vermeer and Reynolds, 1970), with the double-crested cormorant (*Phalacrocorax auritus*) (Kury, 1969), with the white pelican (*Pelecanus erythrorhynchos*) (Anderson *et al.*, 1969), and with the brown pelican (P. *occidentalis*) (Blus, 1970).

These studies frequently show a weak but statistically significant negative correlation between DDE and eggshell thickness, weight, or Ratcliffe's Index, although several studies fail to show such a correlation (Enderson *et al.*, 1982; Wiemeyer *et al.*, 1984). There also appears to be a relationship between some populations that were failing and high levels of DDE; where populations of the same species were not failing, low levels of DDE were reported. For example, in the California channel islands, brown pelicans failed completely to reproduce in 1969 and 1970 (Risebrough, 1971) and showed very high levels of DDE in their eggs. Brown pelicans in Florida, however, reproduced normally and showed low residue levels (Blus, 1970). There were, though, several anomalies. Peregrine eggs in Northern Canada, for instance, contained residue levels at least twice as high as the failing population of peregrines in Great Britain, yet the Canadian peregrines reproduced normally (Enderson and Berger, 1968). In Florida, a population of brown pelicans which had low residues showed a stronger statistical correlation between DDE and shell thickness than the California population, which contained high levels of DDE and 35% shell thinning (Risebrough, 1971).

Nevertheless, in consideration of much of the evidence, it seemed logical to propose that DDT or its metabolites could be involved in reproductive failure. All of the field evidence, however, was correlative in nature only and did not elucidate the physiological basis for this presumption.

Accordingly, laboratory studies were undertaken in an attempt to provide the cause and effect link between DDE and the field observations. Peakall (1967, 1970a) suggests that a reduction of steroids which are necessary for reproduction occurred in the presence of DDT and DDE. One of the primary events in avian reproductive endocrinology is anterior pituitary production of the gonadotropic hormones, follicle stimulating hormone (FSH), and leutinizing hormone (LH). The ovary is in turn stimulated and produces estradiol, progesterone, and testosterone, of which estradiol is the principal product and increases the amount of calcium in the medullary fraction of the longbones (Simkiss, 1967).

Peakall (1970a) proposed that it was primarily the inhibition of estradiol which resulted in the production of thin eggshells. The production of estradiol serves as a feedback mechanism according to which less FSH and LH are produced in egg-laying birds (Sturkie, 1965). If, therefore, low levels of DDE reduce circulating estradiol, it would be expected that the feedback mechanism would result in maintenance of estradiol levels. However, in species that were kept on a calcium-deficient diet, that were fed high doses of DDE, and that laid thin-shelled eggs, no reduction in medullary bone formation was noted (Bitman et al., 1969). Although the theory of estradiol inhibition received initial acceptance (Hickey and Anderson, 1968; Fyfe et al., 1969; Cade et al., 1971), it was subsequently discarded, even by its proponent (Peakall, 1970a).

At the same time another theory, that of carbonic anhydrase (CA) inhibition by DDE was advanced, principally by Bitman et al. (1970) as well as Peakall (1970a, 1970b).

Peakall (1970a) reported that DDE can cause a reduction in both estradiol and CA in paired ringdoves (Streptopelia risoria). Simultaneous with introduction of DDE, however, the light-dark regime was changed from 16 hr. light and 8 hr. dark to 8 hr. light and 16 hr. dark. This change could itself account for endocrine changes because increasing photoperiod is important in stimulation of reproductive events (Sturkie, 1965). Bitman et al. (1970) also reported a reduction in CA activity, in this case in the shell gland of Japanese quail (Coturnix coturnix japonica) that were fed 100 ppm of DDT for three months. In reference to the results of these studies, Dvorchik et al. (1971) state:

> No direct studies of inhibition were done; the shell gland or oviduct of treated birds had about 60% (Peakall, 1970) or 18% (Bitman et al., 1970) reduction in enzyme activity when taken for in vitro analysis. This is not usually enough reduction for physiological inhibition (Maren, 1967); on the other hand it is an unsatisfactory way to investigate inhibition, because drug and enzyme are analyzed together.

Dvorchik et al. (1971) report their own in vitro work, which shows that levels as high as 100 μg/ml of DDT or DDE show no inhibition of CA activity. Pocker et al. (1971) also questions the CA inhibition theory and suggests that DDT and DDE are not inhibitors of CA but simply have the ability to coprecipitate minute amounts of enzyme from solution. Moreover, CA is present in the shell gland and in other tissues in excess amounts (Matsumura, 1975), which would render it unlikely that small amounts of chlorinated hydrocarbons would have an ecologically deleterious effect.

Miller et al. (1976) suggest that DDE inhibits CA ATPase in the shell gland. This conclusion was based on studies with ducks and poultry exposed to 40 ppm DDE in their diet. This suggestion finds support from Bird et al. (1983) who exposed kestrels (Falco sparverius) to 20 ppm DDE and who hypothesize that shell thinning results from changes to the shell gland rather than to the supply of calcium to it. This hypothesis is supported by Lundholm (1987) who "suggested" as a "working hypothesis" that the direct effect of DDE is by reducing secretion or translocation of calcium from the mucosal cells of the shell gland. This hypothesis is derived from studies with two species of ducks exposed to 40 ppm DDE.

In addition to the laboratory studies undertaken to determine the mode of action of DDE, a series of laboratory feeding studies were undertaken to demonstrate eggshell thinning. These included experiments with kestrels (Porter and Wiemeyer, 1969; Wiemeyer and Porter, 1970; Lincer, 1975), with screech owls (Otis asio) (McLane and Hall, 1972), with ducks (Heath et al., 1969; Longcore et al., 1971a, 1971b), and with quail and finches (Bitman et al., 1969; McBlain et al., 1974; Jeffries, 1971). A variety of results were reported from these laboratory studies including an increase in shell weight (Jeffries, 1971) or no change in reproductive parameters (McBlain et al., 1974), but many show a decrease in shell thickness or weight. It was apparent, however, that only the predatory birds studied were evidently sensitive to DDT or DDE at exposure levels approximating environmental levels. Other kinds of birds exhibited varying responses but only at exposure levels greatly exceeding environmental levels.

In the kestrel studies, Weimeyer and Porter (1970) exposed domestically raised kestrels to 2.8 ppm DDE (wet weight basis) and demonstrated a mean shell thinning of 9.7% after two years' exposure. Lincer (1975) also exposed domestic kestrels to 0.3, 3.0, 6.0, and 10 ppm (wet weight basis) of DDE and significant eggshell thinning occurred after exposure to 3.0 ppm.

With the exception of the screech owl study (McLane and Hall, 1972), which exposed the test birds to 10 ppm of DDE resulting in 13% thinning in the second year of the study, no other laboratory studies have been conducted with predatory birds.

III. STATEMENT OF THE PROBLEM

In 1968, all of the published ecological studies which related DDT to reproductive failure in avian predators were based on surveys: that is a few eggs were collected from a given species over a wide geographic range and usually during one breeding season. Moreover, the results of these studies were in some cases contradictory; and in instances where a correlation between DDT and a selected eggshell parameter was found, the correlations were generally weak. I therefore considered that an intensive study of the suspected relationship between DDE and eggshell breakage was important and timely.

The null hypothesis assumed was that DDT and its principal avian metabolite DDE do not influence reproductive success through reduction of the eggshell. The primary test of the hypothesis was analytical determination of chlorinated hydrocarbons in the eggs and the statistical relationship between these and a selected eggshell parameter. To further test the hypothesis, I also considered it important to compare certain environmental factors which influence reproductive success with levels of chlorinated hydrocarbons in the eggs.

I decided that the population of birds used as a vehicle to test this hypothesis should have the following properties:

1. it should be near or at the top of a food chain and therefore possess the potential to accumulate lipophilic compounds,
2. it should be a common and colonial bird, thereby allowing collection of relatively large sample sizes,

3. it should be stenophagus, thereby allowing determination of the source of any chlorinated hydrocarbons,

4. it should be a bird for which there was a reasonable amount of published scientific information,

5. it should contain high levels of DDT contamination, and

6. it should breed in an area where disturbance from industry, recreation, and other human activity was minimal.

In 1967 and 1968, the Canadian Wildlife Service conducted a survey of several species of prairie birds and showed that common terns, nesting at Chip Lake, Alberta, contained high egg DDE residues (Vermeer and Reynolds. 1970). Besides being colonial and abundant, the common tern is a stenophagus terminal predator. There was also a substantial amount of scientific information available regarding it (Palmer, 1941; Austin, 1953). Accordingly, this population of birds met all of the study requirements. Because common terns do not normally return to their breeding grounds until their fourth year (Austin, 1953), the colony was studied for a period of four years, from 1969 to 1972.

IV. METHODS AND MATERIALS

THE STUDY AREA

Chip Lake (Fig. 1) has an area of 150 km^2, is situated 120 km due west of Edmonton, and is underlain by the Edmonton Formation of Late Cretaceous Age, which is of fresh brackish water origin and composed of bentonitic sandstones, sandy shales, bentonitic clays, and coal seams (Twardy and Lindsay, 1971). In most places, the lake is only a few meters in depth and usually turbid. It is drained by the Lobstick River which ultimately empties into the Arctic Ocean.

Although it is close to population centers, virtually no recreational use is made of Chip Lake except for waterfowl hunting in the fall and a very limited amount of sport fishing. Presumably this lack of recreational use is because of the shallow and turbid nature of the water and the lack of other recreational opportunities. Hence the lake is nearly devoid of human presence.

Many of the numerous islands in the lake are several hectares in size and support extensive floral populations of which balsam poplar (Populus balsamifera) is the climax species. One of the larger islands supports a colony of 60-65 pairs of great blue herons. Only two of the islands, however, are suitable for nesting by common terns. These lie beside each other approximately in the middle of the lake and consist of teardrop-shaped gravel deposits left

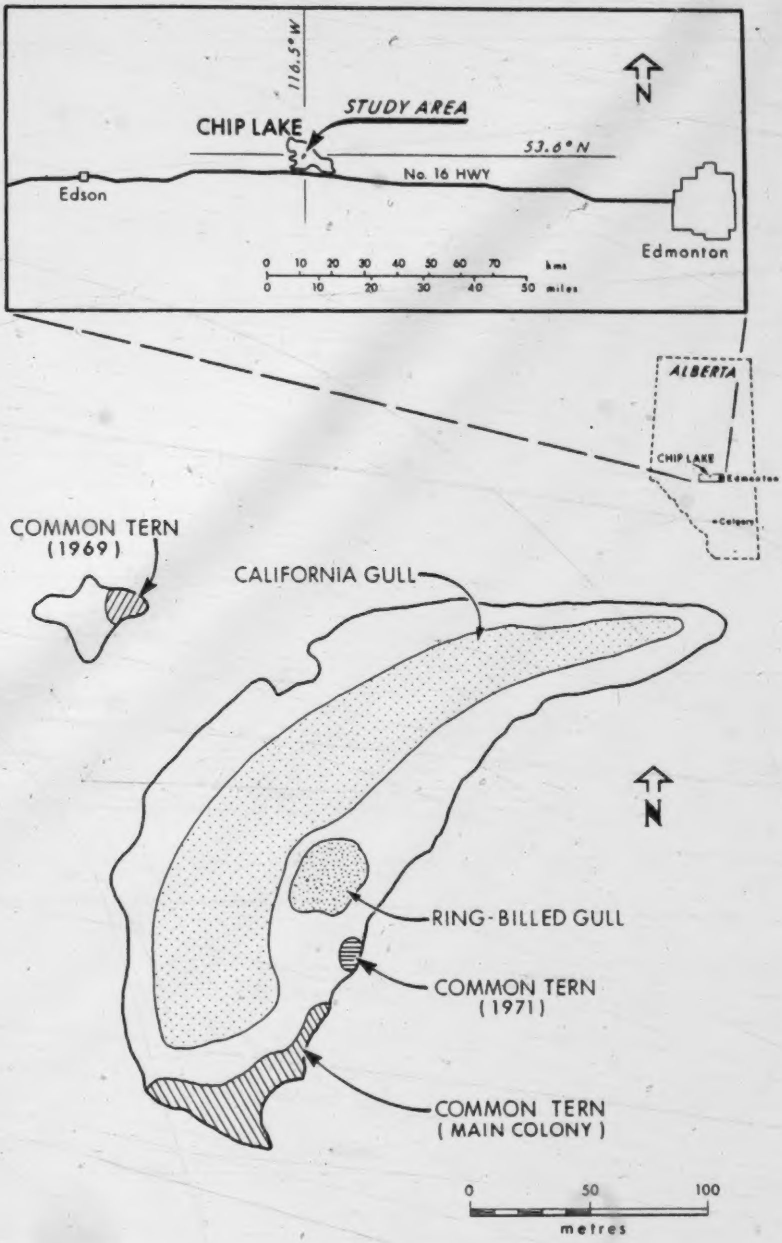
116.5° W
STUDY AREA
CHIP LAKE
53.6° N
N
No. 16 HWY
Edson
Edmonton
0 10 20 30 40 50 60 70 kms
0 10 20 30 40 50 miles
ALBERTA
CHIP LAKE
Edmonton
Calgary
COMMON TERN (1969)
CALIFORNIA GULL
N
RING-BILLED GULL
COMMON TERN (1971)
COMMON TERN (MAIN COLONY)
0 50 100
metres

FIGURE 1 Study Area at Chip Lake, Alberta, Canada and Nesting Zones of Common Terns, 1969-1972

by the retreating Continental Ice Sheet of the last glacier (Grovenor and Bayrock, 1955).

Although common terns attempted to establish a colony on the smallest of these islands in 1969, only one colony on the larger island was occupied during each year of the study (Fig. 1).

The terns share the island with California gulls (*Larus californicus*), ring-billed gulls (*L. delawarensis*), a few pairs of Canada geese (*Branta canadensis*), a variety of other waterfowl, and a few songbirds.

At the turn of the century, white pelicans were abundant nesters on the larger island: hence the name Pelican Island. According to local residents, however, pelicans abandoned this island during the 1920's. Nevertheless, each spring a flock of about 40 white pelicans was observed resting for a few days on the sheltered east side of Pelican Island.

FIELD STUDIES AND SAMPLE COLLECTION

A base for field operations was established on the west side of the lake; the study area was visited, weather permitting, about four times per week from the first of May to the end of August for all four years of the study. Because of concern for the negative influence of human presence on reproductive success, an effort was made to keep each visit to the colony as short as possible, especially in very hot or inclement weather. If more time was required, the colony was left and returned to later in the day.

During each investigation, the entire colony was searched in a north-south direction. All eggs at each nest site were marked with waterproof ink. The nests were recorded as 1, 2, 3... and the eggs were numbered with the nest number and 1, 2, or 3, denoting the sequence in the clutch. For example, the 2nd egg laid in the 15th clutch was recorded as 15-2. All data were recorded in field note books and transcribed onto master data sheets.

A few days after hatching, tern chicks hide in the dense vegetation, making it difficult to record all events and simultaneously keep time spent on the colony at a minimum. In 1969, 1 m diameter circles were constructed of 1 cm square wire mesh in an attempt to solve the problem of tracing chicks after hatching. This technique was abandoned because it was difficult to secure the rings on the uneven substrate, and many chicks escaped. The most suitable method for following chicks through to fledging was banding them with colored plastic bands, the numbers of which were recorded to correspond to the original nest site. When the chicks were old enough to accept U.S. Fish and Wildlife Service bands, these were applied.

When eggs were collected the date, nest, egg number, and other relevant data were recorded. The egg was then wrapped in aluminum foil, placed in a glass jar with an aluminum foil-lined top, labelled, placed on dry ice, and transported to a freezer for later analysis.

During each visit to the colony, observations respecting weather, water levels, plant emergence and growth, and behavior were made. In 1969 and 1970, minnows dropped by adults or regurgitated by chicks were found in the colony and collected. Each of these collections was comprised of about 25 g of fish and were handled in the same manner as the egg collections.

LABORATORY STUDIES

The author either conducted or supervised all analytical work in the South Laboratory of the Department of Food Science except that fish samples were analyzed at the Dairy and Food Laboratory of the Department of Agriculture, Edmonton, Alberta. Though the methods and materials employed in this analytical research have been reported elsewhere (Switzer et al., 1971 and 1973), the analytical and experimental techniques that were employed are described in detail here.

Apparatus

1. Gas-liquid chromatographs: Aerograph models 204 and 1800 gas chromatographs with 250-mcurie tritium ionization sources were used. Five-foot Pyrex columns, 3 mm outer diameter (o.d.), were packed with 10% Dow Corning (DC) 200 and 15% QF-1 (1:1) on Anakrom ABS (60-80 mesh). Replicate samples were analyzed using 5% SE 30 on the same solid support to facilitate resolution of certain peaks. Prepurified nitrogen at a flow rate of 70 ml/min and isothermal operation of 185°C were used in all the routine analyses.

2. Chromatography columns: Pyrex tubes, 28 mm o.d. x 600 mm, with teflon stopcocks, coarse-fritted glass plates, and 1-liter removable reservoirs were used for separation of chlorinated hydrocarbons from the sample tissue.

Reagents

1. Florisil (Fisher Scientific): The florisil, 60-100 mesh, pre-activated at 649°C, was reactivated overnight at 300°C before use and partially deactivated for 48 h with 3% redistilled water (Jonasson, 1968). (In 1969, the florisil was reactivated at 130°C. However, in 1970, a contaminant was discovered which originated in the polyethylene container in certain batches of florisil. Reactivation at 300°C eliminated the source of contamination and did not influence recovery. This temperature was therefore used for reactivation in 1970, 1971, and 1972.)

2. Solvents: Acetone, reagent grade; n-hexane, pesticide grade (Fisher Scientific); petroleum ether, reagent grade; re-distilled (boiling point (b.p.) 60°-80°); and methylene chloride, reagent grade, redistilled (b.p. 40.2°) were used in the extractions.

3. Insecticide standards (Chromatographic Specialties, Brockville, Ontario): Lindane, heptachlor, aldrin, heptachlor epoxide, p,p'-DDE, dieldrin, o,p'-DDT, p,p'-DDD, and p,p'-DDT were used as reference standards to quantitate the chromatograms. Standard polychlorinated biphenyls (PCB's), Arochlor

1254 and 1260 (supplied courtesy of the Monsanto Chemical Co., Chicago, Ill.) were used as PCB reference standards.

Procedures

1. Pesticide residue extraction: Three basic techniques for extraction were available: a wet weight basis, a dry weight basis, or a lipid weight basis. In the wet weight analysis, a sample of the fresh tissue or egg is used for extraction and the result therefore reflects the level of chlorinated hydrocarbons in the whole living tissue or egg. In the dry weight analysis, the sample is dried prior to extraction and the results therefore express the level of chlorinated hydrocarbons concentrated by a ratio of dry tissue weight to living tissue weight. In the case of an egg, this ratio is approximately 4:1 (Newton and Bogan, 1978). In the lipid weight extraction, the lipid is extracted from the sample prior to analysis and the results therefore express the level of chlorinated hydrocarbons concentrated by a ratio of lipid in the living tissue to the whole living tissue. In eggs, this ratio varies from 15:1 to 20:1, depending upon the lipid content of the egg (Newton and Bogan, 1978; Carey et al., 1980).

In this study, there was no imperative to use dry weight analysis because refrigeration was available. There was also no reason to use a lipid weight method since frequency of collection precluded desiccated samples. Moreover, the extra step in each introduces a possibility for error and the conversion factors of dry or lipid weight to wet weight are approximations.

Accordingly, I believed that a wet weight analytical extraction procedure would be more accurate and the following procedure was developed.

The procedure was based on that of Langlois et al. (1964) with some modifications. The egg yolk and white were homogenized in an Ivan Sorval Omni-mixer and 5 g of the homogenate were transferred to a mortar containing 50 g of florisil and ground to a free-flowing powder. This was added above 50 g of florisil prewashed with methylene chloride and petroleum ether (1:1, v/v) in the chromatographic column. Utensils were washed twice with 100 ml of eluting mixture, petroleum ether, and methylene chloride (4:1, v/v) and these washes added to the column reservoir. The eluate was collected in a 1-liter round bottom flask, flash evaporated to dryness, and the residue dissolved in 10 ml of n-hexane.

2. Gas chromatography: Known volumes, 10 µl of the hexane solution from the clean up eluate, were injected into the gas chromatograph. Many factors influence accurate peak height and peak areas in electron capture such as foil contamination, nonlinear attenuation, gas leaks at the injection port, spaces in the column arising from improper packing, temperature change or N_2 flow rate change, etc. Accordingly, on each day of analysis, a standard sample was injected—or a series of standard samples were injected—on a trial and error basis until a peak height of about 90% of full scale deflection was achieved with maximum separation of standards on a stable baseline (Figure 2). It was often necessary to repeat this procedure several times a day.

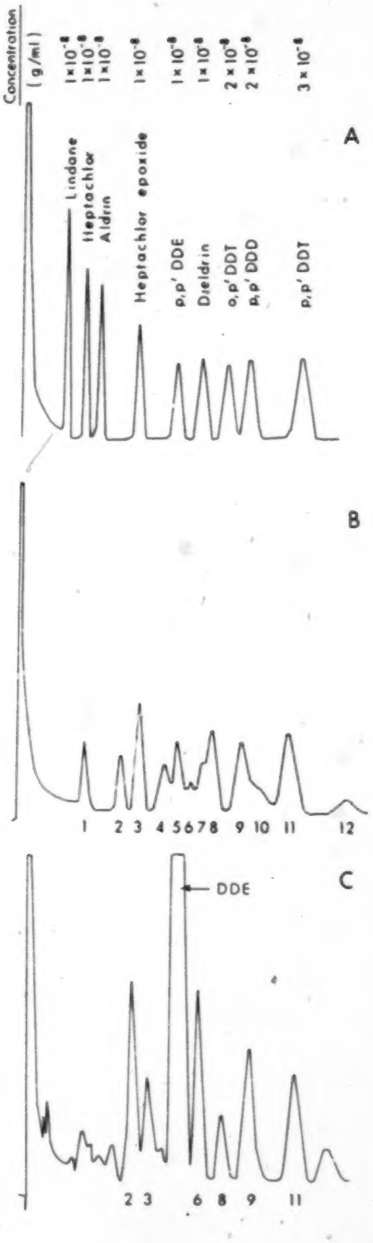

FIGURE 2 Gas chromatograms from a 10% DC200, 15% QF1 column illustrating (A) a 10-µl injection of a standard pesticide mixture, (B) the isomers eluted from a 10-µl injection of 10^{-6} g/ml Arochlor 1254, and (C) an initial 5-µl injection from a tern egg extract. The numbered peaks correspond to PCB's in B, and DDE with the same peak in A.

Egg samples were then injected and a standard was injected for every three or four egg samples. If an egg sample was particularly contaminated and left scale at a given attenuation, the sample was reinjected, after baseline stabilization, at a lower attenuation.

3. Recognition of PCB's: When I began to analyze egg samples in 1969, there were certain peaks on the gas chromatograms which did not always conform to the pesticide standards. These unknown compounds were detected in the summer of 1969 while I first experimented with the N_2 flow rate and the column temperatures to achieve optimal separation of the chlorinated hydrocarbons in the egg samples and the pesticide standard. By increasing the flow rate or column temperature, the elution or retention time is decreased and this results in sharper peaks. However, two compounds with very similar structural characteristics may be eluted at the same time. Conversely, decreasing the flow rate or column temperature increases retention time and separates compounds which are structurally similar but result in flatter peaks, the areas of which cannot be accurately measured.

Although the relative retention times of the standard pesticide mix did not change with temperature or flow rate adjustment, many of the egg contaminants did not always exhibit the same relative retention times when compared to the standard. By experimenting with different liquid phases (5% SE 30, 10% Dow Corning, and 15% QF-1, 1:1, each of which has a different and unique elution profile for DDT and PCB's), I was able to confirm that the only chlorinated hydrocarbon insecticide residue present above trace levels (0.001 ppm) in the common tern eggs was DDE. This left the most probable identification of the other peaks as PCB's.

Accordingly, I prepared two standards of PCB's, specifically Arochlor 1254 and 1260, and was able to confirm that with the exception of DDE, the remaining chlorinated hydrocarbons in the tern eggs were PCB's. Chromatograms of the standard pesticide and the Arochlor 1254 preparation as well as of a tern egg extract are shown in Figure 2.

4. Confirmation of analysis: Thin-layer chromatography (Kovacs, 1963, 1966) was routinely used to validate qualitative identifications achieved by gas chromatography. As well, a number of samples were analyzed on Micro-Tek series GC2000MF equipped with the Dohrmann microcoulometric titration system to further validate identifications. To ensure reliability of results, 10% of the samples in each of 1969 and 1970, chosen at random, were analyzed independently at the Dairy and Food Laboratory of the Department of Agriculture, Edmonton, Alberta. The results of these analyses, when compared by Spearman's rank order correlation coefficient to those of my laboratory, showed a highly significant correlation (r_s=+0.92, P<0.001). In addition, recovery studies were conducted with each lot of new florisil. This was accomplished by adding the standard pesticide mixture and standard Arochlor 1254 and 1260 mixtures to previously analyzed fresh chicken eggs at levels of 0.03 ppm. All insecticides were recoverable within 92% and the PCB's within 90%. To further validate identification of PCB's, several samples were analyzed using Reynolds' (1969) and Armour and Burke's (1970) techniques.

5. Egg collection and storage: Eggs were collected between May 18 and July 20 with the majority being collected in the first 2 weeks of this period. The whole egg was placed in a glass vial with a wax-lined screw cap and immediately frozen on dry ice until analysis. In 1969 and 1970, samples of broken, cracked, abandoned, and otherwise non-viable eggs were collected. For each year of the study, a sample of fresh, viable eggs was randomly collected throughout the season.

Since a wet weight analytical technique was used, eggs that showed marked desiccation or whose contents were only partially present were not analyzed. The frequency of egg collection precluded a high occurrence of desiccated samples and only a few eggs were regarded ineligible for analysis.

6. Eggshell measurements: Three methods were available to determine the quality of the eggshell: thickness, weight, or Ratcliffe's Index (R.I.). I chose to measure thickness because it seemed a more direct measure of relative eggshell strength than the indirect measure of weight or R.I. Before adopting this technique, however, I compared a sample of eggshells with and without the eggshell membrane to ensure that variability in thickness was not influenced by thickness of the membrane.

Thirty-seven eggshells collected in 1969 were measured in two places at the equator and once at each end using the Lewin (1970) method. Membranes were then removed by immersion of the shell in 1:1 lysol and water. They were rinsed and the softened membrane removed. After drying, the eggshell was measured in the same four places. Both samples were highly correlated ($r_{xy}=+0.91$, $P<0.001$). For the remainder of the study, therefore, eggshells and membranes were routinely measured using the technique developed by Lewin (1970).

In 1970, all of the eggshells were also weighed to 0.0001 g with a Mettler gramatic analytical balance in order to compare the Chip Lake eggshells with the weights of 39 pre-1947 eggshells from Western Canada (source: the National Museum of Canada, Ottawa).

7. Statistical analysis: Statistical descriptions used were, for the DDE data: arithmetic mean ($\bar{x}$), geometric mean (G.M.), and range; for the eggshell data: arithmetic mean, standard deviation (s), and range.

Statistical comparisons of the data were performed by comparing DDE to shell thickness between years, within years, between failure and control groups, within the clutch sequence, and between selected levels of DDE. The statistical tests used took into account the skewed distribution of the independent variable, and log transformation of the DDE data was performed where necessary. The tests used were Students t test (t), one way analysis of variance (ANOVA), Pearson's product moment correlation coefficient (r_{xy}), Spearman's rank order correlation coefficient (r_s), Duncan's multiple range test, Wilcoxson's signed rank test, and two sample z test for proportions. Techniques followed Siegel (1956), Steel and Torrie (1960), Snedecor and Cochran (1965), Montgomery (1984), and Miller (1986).

V. RESULTS

BREEDING CHRONOLOGY

Arrival and Nesting

I defined "arrival" as that period of time when common terns were observed in the study area and exhibited breeding behavior as described by Palmer (1941). During the four years of study (1969-1972), arrival occurred on May 12, May 10, May 13, and May 12 respectively. For each year of the study, nesting occurred on the areas shown in Figure 1. With the exception of 1970 and 1972, nests were initiated on more than one part of the study area. This is noted and these small colonies are referred to as "satellite colonies."

Initiation of Egg Laying

Initiation of egg laying in the colony was the day when the first egg was laid in the first nest and this was followed immediately by egg laying in other nests (Figure 3). For each year of the study, initiation of egg laying occurred about one week following the terns' arrival. In 1971, however, egg laying was delayed for a few days, presumably because of high winds, rain, and cold which characterized the weather that spring.

In 1969, the colony was comprised of about 120 pairs of adults; in 1970 of about 240; in 1971 of about 180; and in 1972 of about 160. These estimates are based on the number of nests initiated each year, taking into consideration

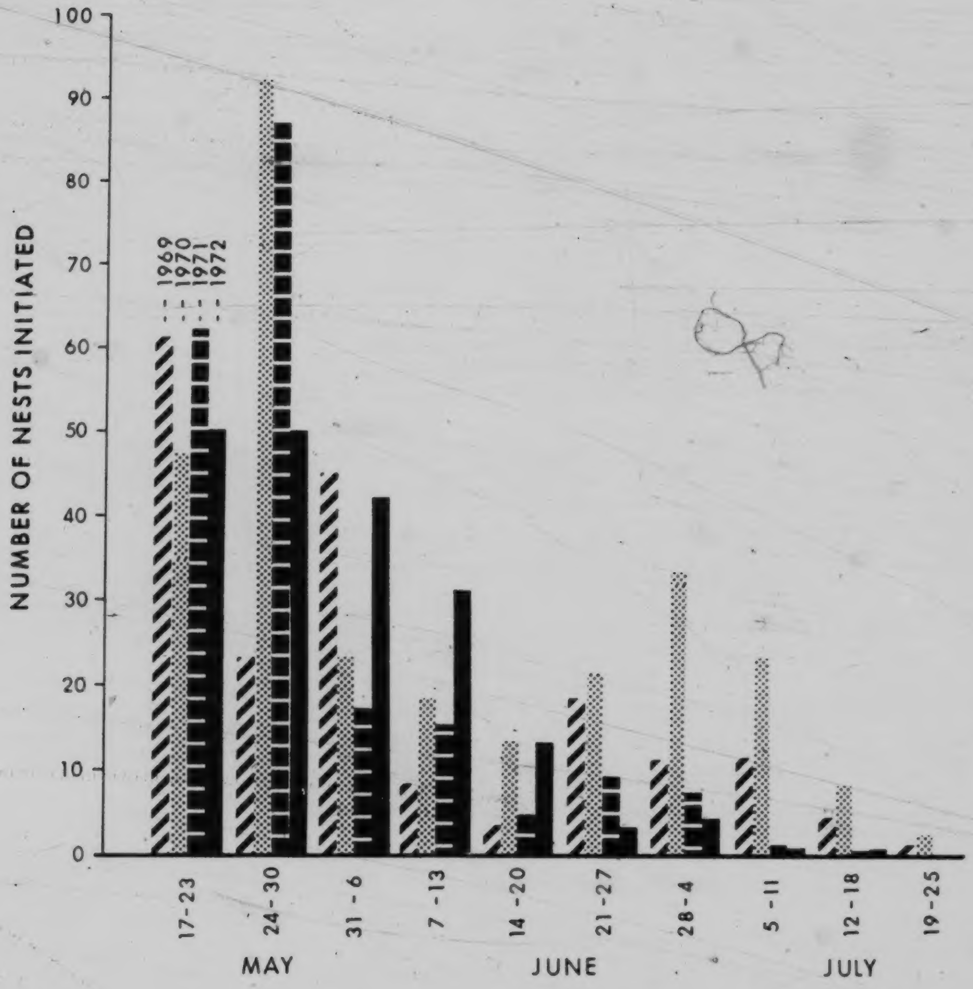

FIGURE 3 Clutch Initiation by Week in 869 Common Tern Nests at Chip Lake, Alberta, 1969-1972

presumed re-nesting attempts as well as visual observation of the terns when they were in the air over the colony.

Clutch initiation peaked in the second week of egg laying (except for 1969), and for all years it peaked by the third week. The last clutch was initiated seven to ten weeks after the first (N=869 nests, Figure 3). During 1969 and 1970, a second peak of nesting activity was observed in the latter part of June. These nests were considered to be mostly re-nesting attempts (Wiggens et al., 1984) and consisted of a much higher percentage of two-egg and single-egg nests than earlier attempts. In 1971, a second peak in activity did not occur because of rising water levels which flooded the colony by the end of June. A second peak was not observed in 1972, also because of rising water levels.

Hatching

Hatching of the first egg in a clutch began 21-25 days after egg laying, with the chicks in two- and three-egg clutches emerging either on alternate days or successive days, even though eggs are almost invariably laid on alternate days. Chick development is well described by Bent (1921) and Palmer (1941).

Satellite Colonies

In 1969, 18 nests were initiated on the northwest side of a small island 60 m northwest of Pelican Island. These were initiated on May 17 in synchrony with the main colony. All of these attempts were either abandoned or washed away and no other attempts were made to nest on this island.

In 1971, 35 nests were initiated 25 m north of the main colony (Figure 3), beginning on June 30. Thirty-three of these nests were initiated between June 30 and July 2, with two on July 17. The sequence of laying and hatching was identical to that of the main colony's.

REPRODUCTIVE SUCCESS

The primary objective of this study was determination of the relationship of DDE to eggshell thickness and ultimately to evaluate the relationship of DDE and shell thickness in reproductive success.* Although ecological parameters were considered important, collection of data in pursuit of the primary objective meant that a substantial amount of time was spent in the vicinity of the nesting terns. The extent of this human presence in influencing both hatching success and fledging success is unknown; it is, however, presumed that this was significant. Accordingly, data with respect to hatching and fledging success should be viewed within this consideration.

Clutch Size

Clutch size was recorded only from nests which were considered complete (Table 1). The mean clutch size of 815 nests was 2.32 with 2-egg and 3-egg clutches comprising about 46% and 43% of all clutches initiated. The remainder were one-egg clutches. An apparent increase in clutch size existed from 1969 to 1972. Relatively more one-egg and two-egg clutches were laid in

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* Reproductive success is the number of birds fledged per nest and is discussed on the basis of hatching success (number of eggs hatched per nest) and fledging success (number of birds fledged per nest). Accordingly, fledging success is synonymous with reproductive success.

TABLE 1 Clutch Size in 815 Common Tern Nests at Chip Lake, Alberta, 1969-1972

	1 Egg	2 Eggs	3 Eggs	Clutch Size
1969	17 (11%)	89 (56%)	54 (34%)	160 nests 2.25 eggs/nest
1970	38 (14%)	120 (45%)	110 (41%)	286 nests 2.29 eggs/nest
1971	15 (7%)	87 (43%)	101 (50%)	203 nests 2.42 eggs/nest
1972	20 (11%)	76 (41%)	88 (48%)	184 nests 2.37 eggs/nest
Total	90 (11.1%)	372 (45.6%)	353 (43.3%)	815 nests 2.32 eggs/nest

1969 and 1970 than in 1971 and 1972. The opposite is the case with three-egg clutches.

In 1969, the second nesting cycle accounted for 75% of all one-egg nesting attempts and in 1970 for 76% of all one-egg nesting attempts. Morris _et al._ (1976) and Wiggens _et al._ (1984) have established that late nesters and young nesters have lower clutch sizes as well as lowered reproductive success. This accounts for the increased percentage of one-egg nests during 1969 and 1970 when compared to 1971 and 1972 and accounts for the smaller average clutch size observed during those two years.

Hatching Success

During the four years of the study, 714 nests were followed from clutch initiation through to hatching (Table 2). Overall hatching success was 36% or 0.84 eggs per clutch. In 1969, hatching success was 24% (0.5 per clutch), in 1970 42% (1.0 per clutch), in 1971 30% (0.7 per clutch), and in 1972 it was 46% (1.1 per clutch).

Categories of pre-hatching failure for the four years of the study are described as "fractured," "non-viable," "abandoned," "predation," "disappearance," and "other"* (Table 3).

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* Other included eggs which were inadvertently damaged during investigation, eggs found outside of nests, eggs found floating in water, eggs apparently punctured by beaks, and in 1971 by inundation.

TABLE 2 Hatching Success in 714 Common Tern Nests at Chip Lake, Alberta, 1969-1972

	Number of Nests	Number of Eggs Laid/Nest	Number of Eggs Hatched/Nest	Hatching Success %
1969	160	2.3	0.5	24
1970	197	2.3	1.0	42
1971	179	2.4	0.7	30
1972	178	2.4	1.1	46
	714	2.33	0.84	36

TABLE 3 Fate of 1,667 Common Tern Eggs in 714 Nests at Chip Lake, Alberta, 1969-1972

Fate	1969	1970	1971	1972	Total
Fractured	44 (12%)	36 (8%)	49 (12%)	21 (5%)	150 (9%)
Non-viable*		48 (11%)	29 (7%)	5 (1.2%)	82 (6%)
Abandoned	49 (14%)	27 (6%)	31 (7%)	11 (3%)	118 (7%)
Predation	0	12 (3%)	1 (0.2%)	2 (0.5%)	15 (0.9%)
Disappearance	159 (44%)	110 (24%)	89 (21%)	180 (43%)	538 (32%)
Other	22 (6%)	29 (6%)	104 (24%)	7 (2%)	162 (10%)
Hatched	86 (24%)	190 (42%)	131 (30%)	195 (46%)	602 (36%)
Fledged	20 (5%)	110 (24%)	2-3 (0.5%)	105 (25%)	
Total	360	452	434	421	1,667

Eggs laid in the two satellite colonies are excluded from this and all other calculations.

* In 1969 non-viable eggs were included in the abandoned category; therefore only three years' data are available in this category. The summary calculation is expressed on the basis of data from 1970, 1971, and 1972 only.

Fractured eggs were eggs which showed circular indentations of 5-10 mm^2 as well as eggs which showed longitudinal or, occasionally, diagonal cracks, presumably occasioned from a blow by the tarsi of the incubating adult or else rolling against a rock or other egg. Eggs considered to be non-viable were those which had been incubated to term but failed to hatch and those which were incubated normally but were watery.

Predation was noted in a small number of instances, invariably on the periphery of the colony where fractured and partially consumed eggs, characteristic of gull predation, were found.*

Egg disappearance was a major factor in pre-hatching failure. However, I did not directly observe egg disappearance and can only speculate as to its cause. Almost without exception the whole clutch disappeared, leaving no trace. The entire island was searched repeatedly for egg shell remains and none were found. Therefore the eggs were consumed entirely and/or removed entirely from the island. Any significant amount of predation by gulls was ruled out as a cause of disappearance as the colony was vigorously defended by the terns. This defence was to the extent that on two occasions fledgling California gulls which flew over the colony were forced from the air, mobbed, and killed by the terns. Adult gulls were not observed at low altitude over the colony. Besides the resident species of gulls, no other predators were known to inhabit or to visit the island. Accordingly, it is considered that the terns were most likely responsible.

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* In 1970 ant predation was observed to cause failure of two eggs.

In 1969, no eggs were separately categorized as "non-viable" but rather were included in the "abandoned" class. This accounts for the increase in abandonment when 1969 is compared to other years.

An important anomaly in Table 3 is in the "other" category in 1971, where 24% egg failure is recorded. Almost all of this (93 out of 104 eggs) was attributed to inundation and was the major cause of pre-hatching failure that year. This was the only year when egg disappearance was not the major cause.

Fledging Success

In 1969, fledging success was 5% (0.1 per clutch) and in 1970 24% (0.6 per clutch). In 1971 the colony was completely flooded by July 13 and only a few fledglings were observed flying after this date. Fledging success therefore was about 0.5% (0.02 per clutch) for this year. In 1972, fledging success was about 25% (0.6 per clutch).

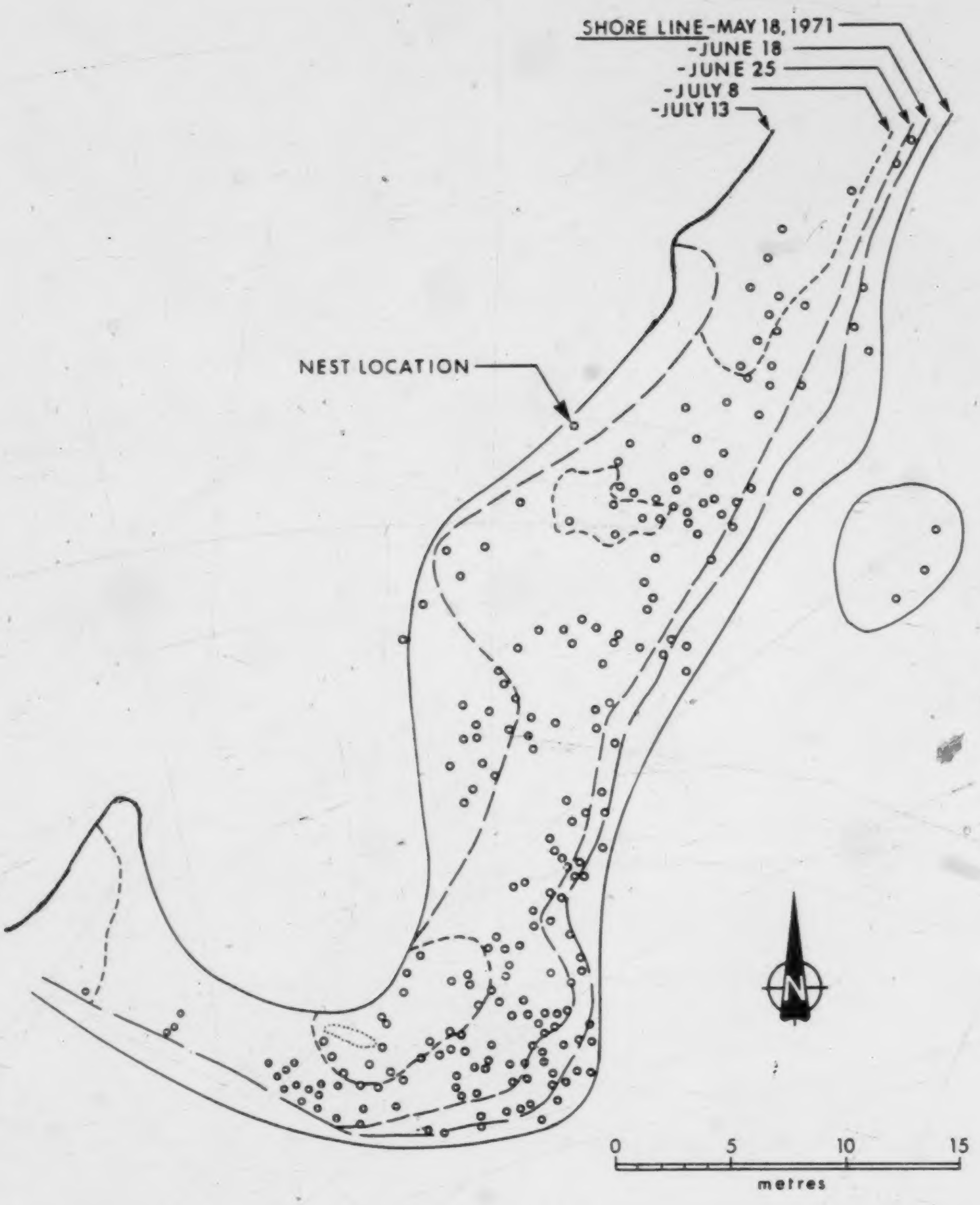
It has been noted that the intensive field investigation probably introduced a disruptive factor which may have had some influence on the ability of the terns to incubate, and therefore hatching success may have been reduced. This disruptive factor likely had a greater influence on fledging success. Tern chicks are precocial at hatching (Winkler and Walters, 1983) and are capable of escape behavior at about three days of age. In response to disturbance, they leave the nest area to hide. The dense vegetation, especially stinging nettles (Urtica gracilis), frequently prevented return to the nest. Because of the closeness of the nests, chicks were frequently observed being attacked by adults on other nests. Of greater consequence, however, were escape attempts into the water. The configuration of the colony dictated that the easiest escape route was into the water, where the chicks swam out and away from the colony. Prevailing winds were from the northwest and occasionally chicks failed to return to the colony.

For the foregoing reasons, it is considered that reproductive success was influenced by investigation and reproductive success was below that which would otherwise have been achieved. Although I was unable to quantitate this impact exactly, I have estimated that it reduced fledging success by 30-40%.

Nest Site Location

By 1971, it was apparent that egg disappearance was a major factor in hatching success; it was also suspected that the terns were responsible. The distance between nests on this colony was closer than is typical for the species (Palmer, 1941), and therefore I mapped nest site locations for 225 nests in 1971 (Figure 4).

The area of greatest nest density was on the southern-most part of the colony. Here distances of as little as 25-30 cm between nests was not uncommon. This nesting pattern was characteristic of each year of the study.


SHORE LINE-MAY 18, 1971
-JUNE 18
-JUNE 25
-JULY 8
-JULY 13
NEST LOCATION
N
0
5
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15
metres

FIGURE 4 Nesting Location of 225 Common Tern Nests at Chip Lake, Alberta, 1971

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CHLORINATED HYDROCARBONS

A total of 300 eggs, representing approximately 16% of all eggs laid, were analyzed during the four-year study; DDE was the only insecticide residue detected above trace levels (0.001 ppm wet weight). Polychlorinated biphenyls were universally present, and I estimated the ratio of PCB's to DDE as 1:9. A random analysis of 20 eggs sampled in each of 1969 and 1970 showed a Spearman's rank order correlation coefficient of +0.79 ($P<0.01$) and +0.82 ($P<0.01$) between DDE and PCB's respectively.

Eggshell Thickness and DDE 1969 - 1972

The measurements of DDE and shell thickness for each year of the study are shown in Table 4 and Figures 5 and 6. DDE decreased each year of the study and shell thickness remained essentially the same. A one way ANOVA was performed to compare the means of both categories. In the case of DDE (log transformed), the resulting F ratio = 6.055 and $P<0.000$. In the case of eggshell thickness, $F=0.91$ and $P>0.25$. Because the 1969 and 1970 samples contained fractured eggs while the 1971 and 1972 samples did not, it is possible that a bias could be introduced into the 1969 and 1970 samples on this account. Accordingly, a one way ANOVA was performed comparing only the non-fractured categories from each year. In this case, DDE (log transformed) resulted in an F ratio of 3.099 and $P<0.05$. Shell thickness showed an F ratio of 1.149 and $P>0.25$. In summary, DDE levels significantly decreased each year of the study while eggshell thickness remained constant.

TABLE 4 Summary of DDE and Shell Thickness
in 300 Common Tern Eggs from
Chip Lake, Alberta, 1969-1972

		1969	1970	1971	1972
		n=68	n=105	n=62	n=65
DDE (ppm)	$\bar{x}$	7.57	4.52	3.59	2.98
		(0.64-104.0)	(0.13-26.17)	(0.02-18.15)	(0.04-16.05)
	G.M.	3.59	2.38	1.88	1.80
Eggshell Thickness (μ)	$\bar{x}$	185	181	181	183
		(147-220)	(114-224)	(141-216)	(130-218)
	s	18	21	17	19

Mean DDE levels are significantly different (ANOVA, F = 6.055, P <0.000)

Eggshell thickness is not significantly different (ANOVA, F = 0.91, P >0.25)

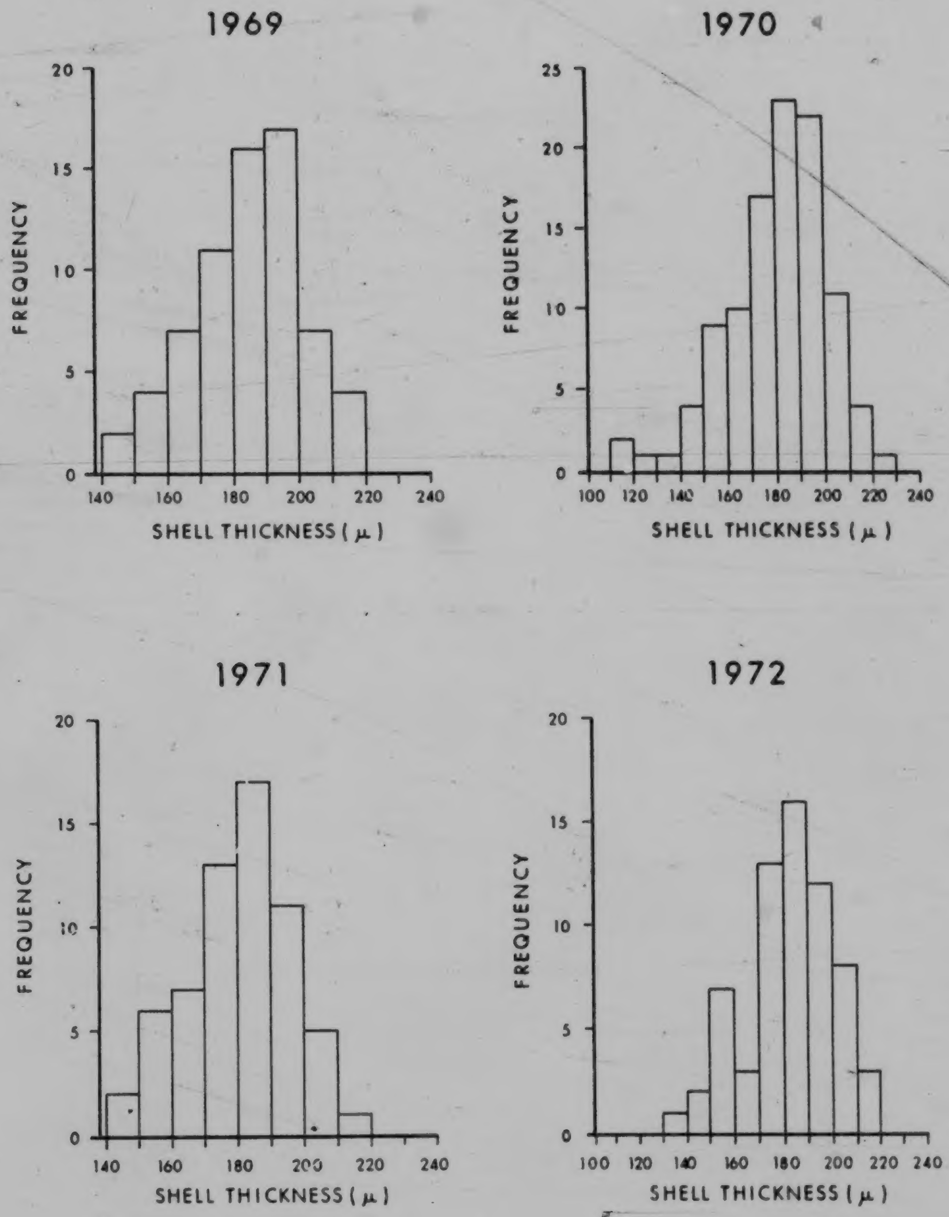

FIGURE 5 Eggshell Thickness in Whole Samples of Common Tern Eggs from Chip Lake, Alberta, 1969-1972

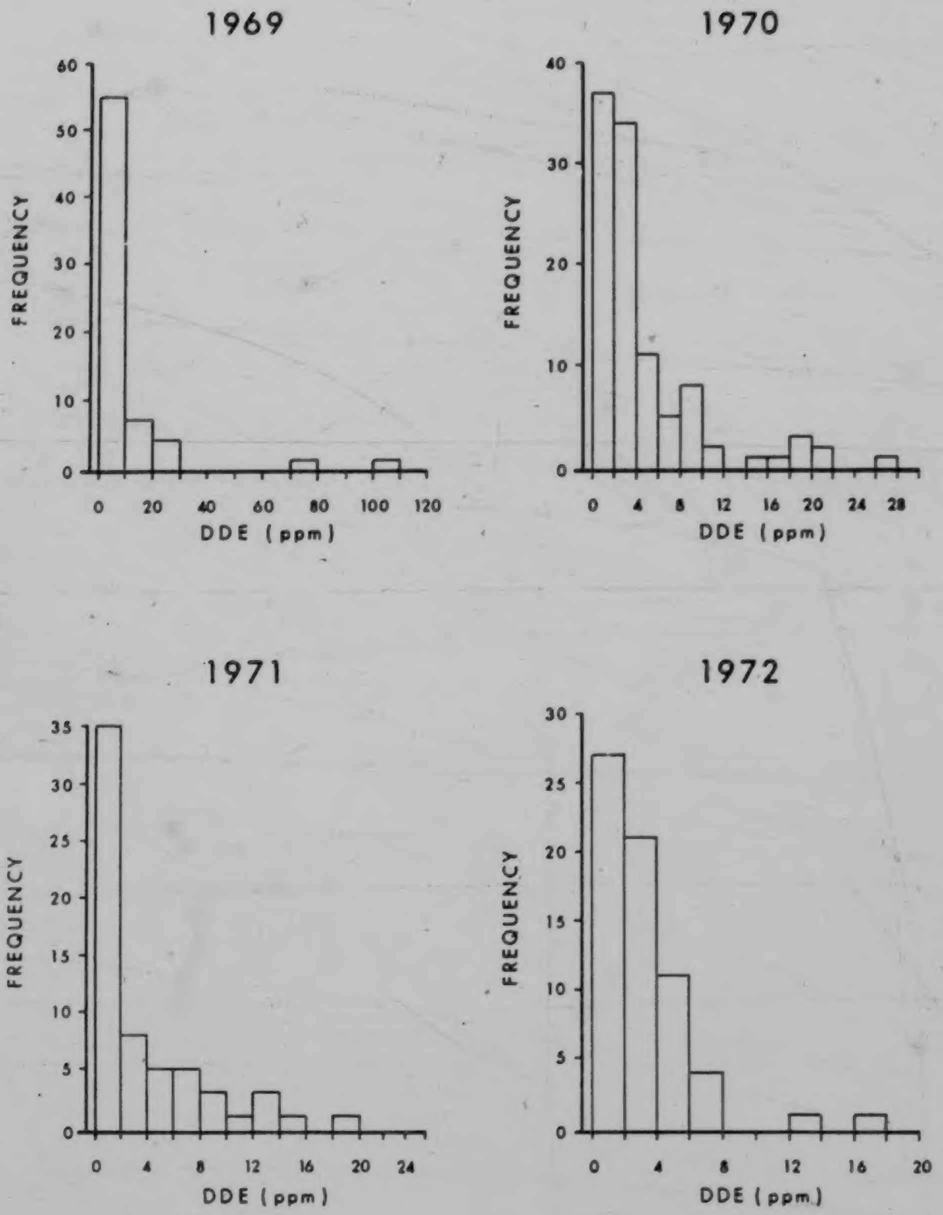

FIGURE 6 DDE Content in Whole Samples of Common Tern Eggs from Chip Lake, Alberta, 1969-1972

Eggshell Thickness and DDE—1969

In 1969, a total of 69 eggs were collected (Figure 7). The mean DDE level was 7.57 ppm (0.64-104.0) and shell thickness was 185 μ (147-220, $s=17$). Spearman's rank order correlation coefficient (-0.027) was not statistically significant.

In Table 5, distinction between fractured and non-fractured eggs collected in 1969 is made. One way ANOVA was calculated to compare the means between fractured and non-fractured eggs. There was no difference between the levels of log DDE or between thicknesses.

Eggshell Thickness and DDE—1970

In 1970, 105 eggs were collected (Figure 7). The mean DDE level in this sample was 4.52 ppm, (0.13-26.17) and the mean shell thickness was 181 μ (114-224, $s=21$ μ). Spearman's rank order coefficient (-0.267) was significant ($P<0.05$).

The 1970 sample was analyzed to determine the difference, if any, between fractured eggs, non-viable eggs, and a control sample (Table 6). If DDE was influencing reproductive success, this would be evident in a comparison of eggs which were structurally damaged during incubation or eggs which were non-viable when either class was compared with the control sample. One way ANOVA was performed to compare the means of the DDE levels and shell thickness for the fractured, non-viable, and control eggs. In the case of DDE levels (log transformed), no statistically significant difference existed ($F=1.340$, $P>0.25$). In the case of shell thickness, however, a statistically

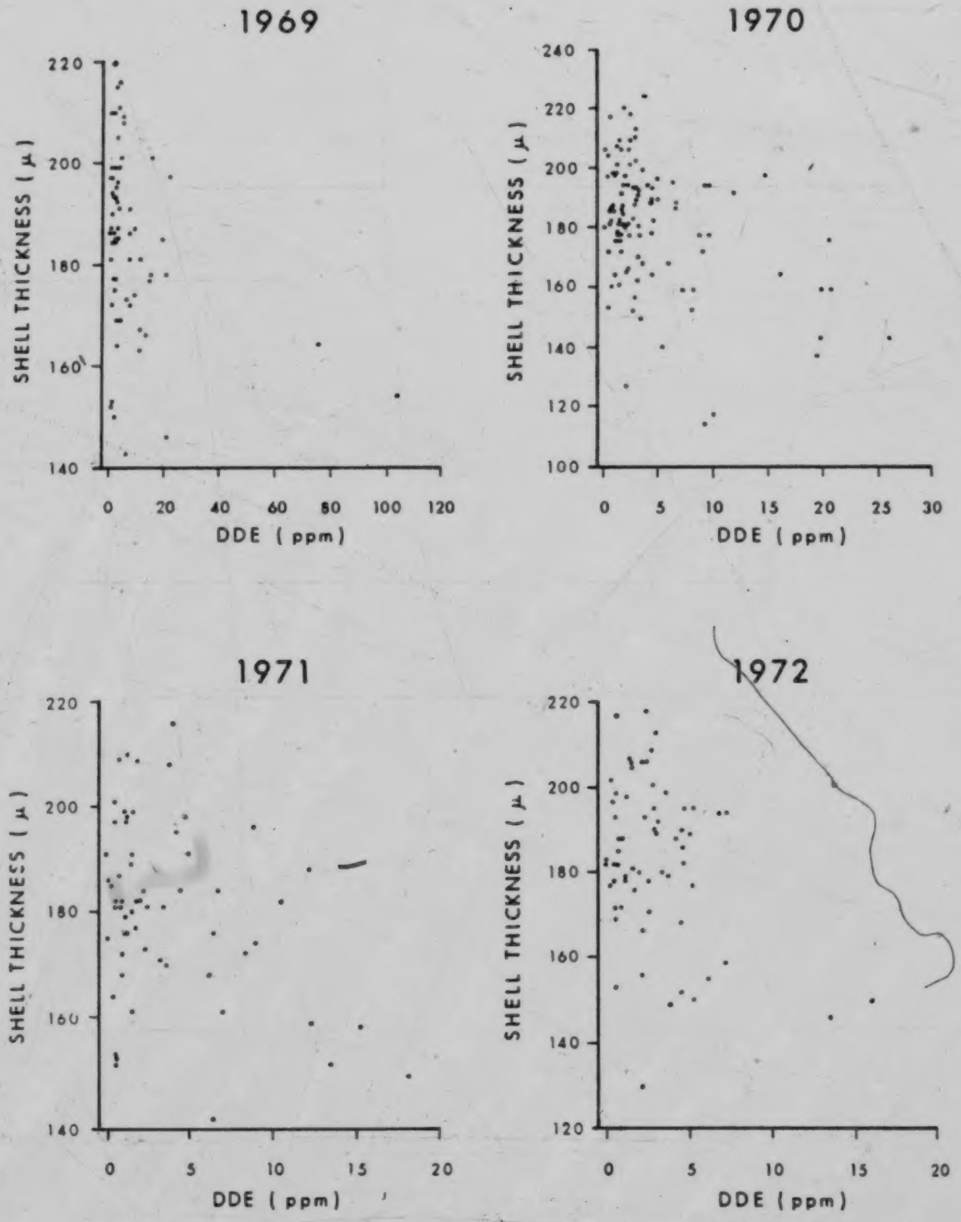

FIGURE 7 The Relationship of DDE to Eggshell Thickness in Whole Samples of Common Tern Eggs from Chip Lake, Alberta, 1969-1972

TABLE 5 DDE and Eggshell Thickness by Category in 68 Common Tern Eggs Collected at Chip Lake, Alberta, 1969

	DDE (ppm)	Thickness (μ)
Fractured	$\bar{x}$ = 6.18	$\bar{x}$ = 184
n = 29	(0.66-21.22)	(147-216)
	G.M. = 3.84	s = 15
Non-Fractured	$\bar{x}$ = 8.99	$\bar{x}$ = 186
n = 39	(0.64-104.0)	(148-220)
	G.M. = 3.59	s = 19

Differences between means of both DDE and thickness are not significant

TABLE 6 DDE and Eggshell Thickness by Category in 105 Common Tern Eggs Collected at Chip Lake, Alberta, 1970

	DDE (ppm)	Thickness (μ)
Fractured	$\bar{x}$ = 5.68	$\bar{x}$ = 170
n = 31	(0.33-20.52)	(117-206)
	G.M. = 3.50	s = 24
Non-viable	$\bar{x}$ = 3.52	$\bar{x}$ = 189
n = 25	(1.11-14.71)	(159-220)
	G.M. = 2.73	s = 17
Other	$\bar{x}$ = 4.40	$\bar{x}$ = 184
n = 9	(0.55-8.13)	(152-224)
	G.M. = 3.25	s = 19
Control	$\bar{x}$ = 4.42	$\bar{x}$ = 184
n = 40	(0.13-26.17)	(143-217)
	G.M. = 2.38	s = 16

Mean DDE levels are not significantly different (ANOVA, F = 1.340, P>0.25)

Mean thickness of fractured eggs is significantly different from other categories (ANOVA, F = 8.944, P<0.000) significant difference existed between the thickness of fractured eggs and of either non-viable or control eggs (F=8.944 and P<0.000). Within these subsamples the fractured eggs and the non-viable eggs did not show a statistically significant correlation between DDE and thickness. The control sample, however, did (r_s= -0.521, P<0.001), which was significant.

Eggshell Thickness and DDE—1971

In 1971, only whole fresh eggs which were first in the clutch sequence were collected. It was considered that since the strongest relationship between DDE and eggshell thickness was in the 1970 control sample, this should be duplicated in 1971 with a larger sample. In addition, rising concern over interference with reproductive success indicated that time spent at the colony should be minimized.

Sixty-two eggs were collected in 1971 (Figure 7). Mean DDE was 3.54 ppm (0.02-18.15) and mean shell thickness was 181 μ (141-226, s=17). Spearman's rank order correlation coefficient (-0.165) was not significant.

Eggshell Thickness and DDE—1972

As in 1971, 65 whole, apparently viable eggs representing the first egg in the clutch sequence were analyzed (Figure 7). The mean DDE was 2.98 ppm (0.04-16.05) and mean shell thickness was 183 μ (130-218, s=19). Spearman's rank order correlation coefficient (-0.116) was not significant.

DDE, Eggshell Thickness, and Position of the Egg in the Clutch Sequence

DDE and eggshell thickness were also compared to the position of the egg in the clutch sequence. If DDE is differentially deposited in the egg over the egg laying sequence, then eggshell thickness in the clutch sequence should increase or decrease with decreasing or increasing levels of DDE in the egg.

In 1969, the position in the clutch sequence was known for 53 of the 68 eggs analyzed (Table 7). A marked increase in DDE occurs from the first to the third egg, but this trend is not evident in shell thickness. A statistically significant difference existed between levels of log DDE and clutch sequence ($F=3.243$ and $P<0.05$), but no statistically significant difference existed between eggshell thickness and clutch sequence ($F=1.036$ and $P>0.05$).

In 1970, the position in the clutch sequence was known for 100 eggs (Table 8). There was no statistically significant difference between levels of log DDE and clutch sequence ($F=1.645$ and $P>0.10$) or between thickness and the clutch sequence ($F=0.452$ and $P>0.50$).

Eggshell Thickness and DDE—Entire Study

In addition to comparing DDE and eggshell thickness between years and categories, the samples for all four years were treated as a single sample (Figure 8). The mean DDE level was 4.74 (G.M.=2.51), the mean eggshell thickness was 182 μ (s=18 μ), and $r_s = -0.181$ which is not significant.

TABLE 7 DDE (ppm Wet Weight), Eggshell Thickness (μ), and Position of the Egg in the Clutch Sequence in 53 Eggs Collected At Chip Lake, Alberta, 1969

	DDE (ppm)	Thickness (μ)
1st Egg n = 22	$\bar{x}$ = 3.82 (0.44-21.15) G.M. = 2.37	$\bar{x}$ = 188 (146-200) s = 18
2nd Egg n = 19	$\bar{x}$ = 11.03 (0.63-75.47) G.M. = 4.97	$\bar{x}$ = 180 (152-201) s = 14
3rd Egg n = 12	$\bar{x}$ = 14.03 (1.53-104) G.M. = 5.60	$\bar{x}$ = 185 (143-216) s = 24

Mean DDE levels are significantly different (ANOVA, F = 3.243, $P<0.05$)

Mean thickness is not significantly different (ANOVA, F = 1.036, $P>0.05$)

TABLE 8 DDE, Eggshell Thickness, and Position of the Egg in the Clutch Sequence in 100 Eggs Collected at Chip Lake, Alberta, 1970

	DDE (ppm)	Thickness (µ)
1st Egg	$\bar{x}$ = 4.31	$\bar{x}$ = 183
n = 53	(0.33-20.66)	(114-220)
	G.M. = 2.35	s = 20
2nd Egg	$\bar{x}$ = 4.69	$\bar{x}$ = 180
n = 31	(0.98-19.67)	(127-224)
	G.M. = 3.36	s = 21
3rd Egg	$\bar{x}$ = 5.27	$\bar{x}$ = 177
n = 16	(0.02-26.17)	(143-204)
	G.M. = 3.40	s = 15

Mean levels of DDE and thickness are not significantly different.

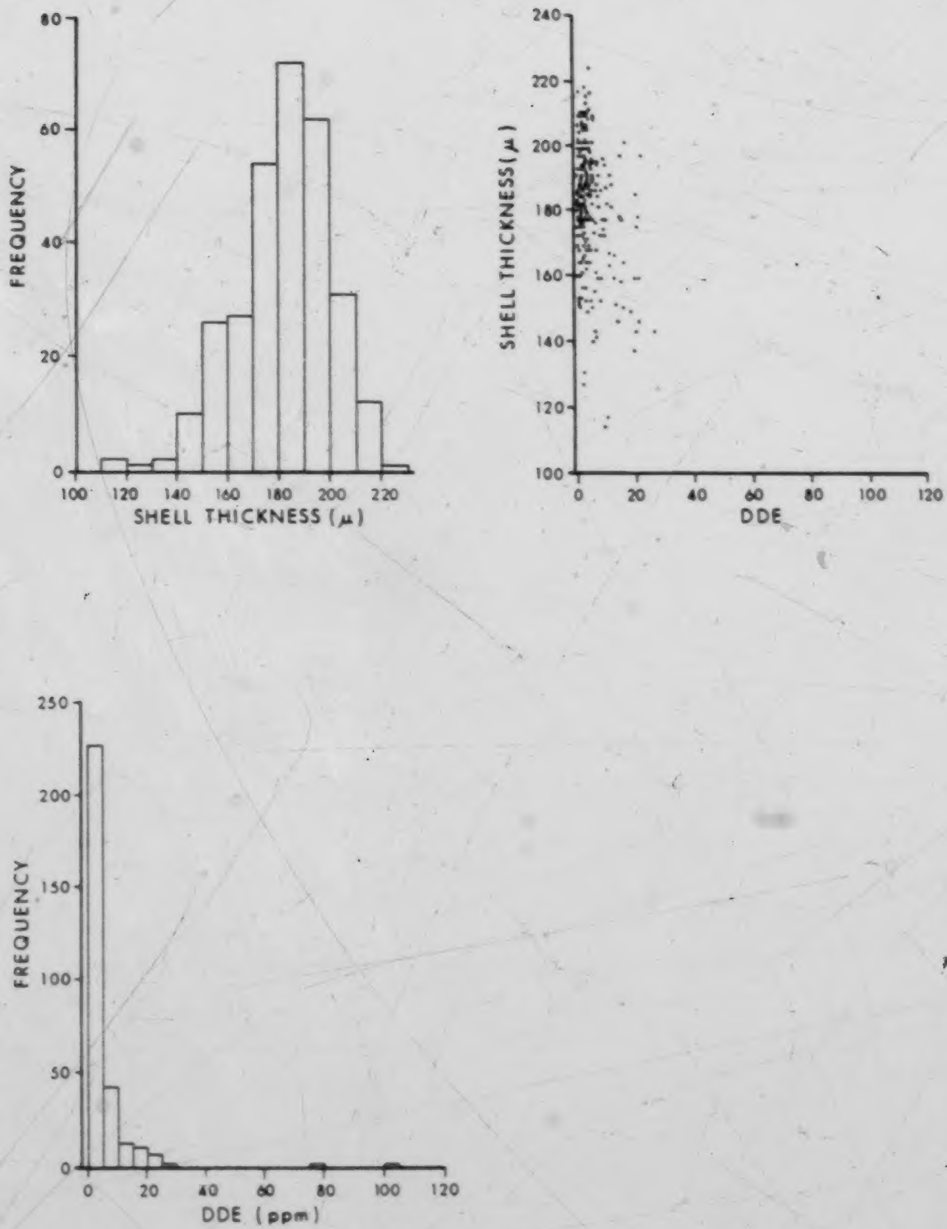

FIGURE 8 Shell Thickness, DDE, and Distribution of 300 Analyses of DDE/Eggshell Thickness in Common Tern Eggs from Chip Lake, Alberta, 1969-1972

All of the DDE/eggshell analyses were combined and evaluated with DDE as the criterion by using 2 ppm, 4 ppm, 8 ppm, and 16 ppm to create five categories (Table 9). Here a comparison of mean thickness was conducted across subgroups using one way ANOVA. This resulted in an F ratio of 10.434 and P<0.001. Pair comparisons using Duncan's Multiple Range test were performed. Subgroups 1, 2, and 3 were not significantly different, and subgroups 4 and 5 were not significantly different. However, subgroups 1, 2, and 3 were significantly thicker than subgroups 4 and 5 at the 0.01 level. In other words, eggshells were found to be significantly thinner in eggs containing more than 8 ppm of DDE.

Table 10 shows a breakdown by year of eggs containing 8 ppm or more of DDE and eggshells which were 170 μ or less in thickness. To compare these data, a two-sample z test for proportions was applied. There is a statistically significant reduction in the number of eggs containing 8 ppm (P=0.0005), but there is no statistically significant change in the number of eggs which are 170 μ or less (P=0.898). Therefore, eggs which were highly contaminated (8 ppm or more) declined significantly each year, but the number of eggs 170 μ thick or less remained constant for the four years of the study.

In summary, DDE significantly declined over the four years of the study, but eggshell thickness remained the same. In one year of the study DDE levels increased with the egg sequence, but this had no effect on shell thickness. Also in one year of the study, eggshell fracture was correlated with eggshell thickness but not with levels of DDE. Of the nine categories of DDE/eggshell

TABLE 9 Comparison of Five Subgroups Created from the Whole Sample of 300 Observations Using DDE as a Criterion: (0-1.99), (2.00-3.99), (4.00-7.99), (8.00-15.99), and (16-) ppm

Subgroup (n)	$\bar{x}$ DDE	$\bar{x}$ Thickness (s)
1. 0 ppm (119)	1.07	185 (15)
2. 2 ppm (87)	2.85	187 (20)
3. 4 ppm (49)	5.58	181 (18)
4. 8 ppm (29)	10.97	170 (20)
5. 16 ppm (16)	28.56	163 (19)

Mean thickness is significantly different across subgroups (ANOVA, F = 10.434, $P<0.001$). Subgroups 1, 2, and 3 are not significantly different and subgroups 4 and 5 are not significantly different, but subgroups 4 and 5 are significantly different from subgroups 1, 2, and 3 (Duncan's multiple range test, $P<0.01$).

TABLE 10 Number of Eggs by Year
Containing 8 ppm or More of DDE
and 170 μ or Less in Thickness

	8 ppm n (%)	170 μ n (%)
1969	16 (22)	9 (13)
1970	18 (17)	23 (22)
1971	8 (13)	15 (24)
1972	2 (3)	12 (18)

Number of eggs containing 8 ppm or more of DDE declined significantly (z test, P=0.0005).

Number of eggs 170μ or less did not decline (z test, P=0.898).

comparison, only two showed a statistically significant association. Finally, highly contaminated eggs significantly decreased each year of the study, but the number of thin-shelled eggs remained the same for each year of the study.

VI. DISCUSSION

The primary objective of my study was to further elucidate the hypothesized relationship of DDE to eggshell thinning in a wild population of predatory birds. As a consequence, a considerable amount of time was spent towards this end on the colony site collecting eggs.

The literature respecting the impact of intrusion on reproductive success in terns is ambiguous. Palmer (1941) states that disturbance can "ruin the nesting" of common terns. Erwin and Smith (1985), in a two-year study of several colonies on the mid-Atlantic coast, conclude that their presence influenced reproductive success—but they did not quantify it. Chapdelaine *et al.* (1985) also conclude, from a common tern study in the St. Lawrence River, that reproductive success would have been higher if their activities had been reduced.

On the other hand, Fox (1976) concludes from a one-year common tern study in central Alberta that his intensive investigation (44 visits) did not impact on reproductive success. Morris *et al.* (1976) intensively studied five common tern colonies on the lower Great Lakes and also conclude that their investigation did not influence reproductive success.

Most studies of common terns, however, do not address the impact of investigation, even though these studies involved frequent intrusion (Hebert, 1985; Custer *et al.*, 1986; Erwin, 1988).

The impact of investigation has, however, been determined in other species of colonial birds. In a two-year (1981 and 1982) white pelican study, Boellstorff _et al._ (1988) found reproductive success to be 0.5 young per nest attempt in a colony investigated for purposes of egg collection for pesticide analyses. In an undisturbed colony in the same year and area, it was 1.2 young per nest. In the second year of the study, neither colony was disturbed and reproductive success was 1.1 young per nest in both colonies.

In a brown pelican study, Anderson and Keith (1980) state that even a single walk through a pelican colony can lead to abandonment or reproductive failure. It is possible that the circumstances of some common tern colonies is such that investigation would not influence reproductive success detectably. It must, however, be a factor in most colonies; and although I was unable to quantitate it at Chip Lake, it was important with respect to fledging success. On the other hand, investigation probably had little impact on chronology, nest site selection, clutch size, incubation, DDE levels, eggshell thickness, or hatching success.

BREEDING CHRONOLOGY, NESTING, CLUTCH SIZE, AND INCUBATION

Common terns arrived in early May each year. As Nisbet (1973a) points out, breeding terns are difficult to count with precision. I am confident, however, that the number of pairs recorded at Chip Lake (120, 240, 180, and 160 respectively) are accurate and that over the four years of study there was no trend to a decreasing or increasing breeding population.

Egg laying began in the third week of May at Chip Lake, which is consistent with initiation of egg laying in Massachusetts (Nisbet, 1973b), Rhode Island (Custer et al., 1986), and North Carolina (Chapdelaine et al., 1985). In the St. Lawrence River, however, egg laying begins in the second week of June (Chapdelaine et al., 1985). I would have expected that the onset of breeding at Chip Lake would not occur in synchrony with colonies as far south as Massachusetts, Rhode Island, or North Carolina but rather would have been in synchrony with colonies at similar latitudes such as the St. Lawrence River, since the onset of breeding in the same species usually occurs later in the season at increasing latitudes (Lack, 1954). The east coast common terns, however, winter on the southern Atlantic coast and the Caribbean (Austin, 1953), whereas the northwestern population of common terns follow a migratory route over the Rocky Mountains and winter on the Pacific coast from California to Peru (Huston, 1972; Switzer et al., 1973). Therefore, there may be differential factor(s) other than latitude which influence the onset of nesting between the eastern and western populations of common terns.

Nesting at Chip Lake was characterized by a well-defined peak in late May, followed by a less well-defined peak in late June. Most authors report this cycle, and the second peak is generally attributed to renesting attempts and to first attempts by young birds (Nisbet, 1973a). Nesting also occurred on what I called satellite colonies, once in 1969 and once in 1971. In the 1969 satellite colony, nesting began in mid-May and I presumed that these were members which had been displaced by some unknown factor from the main colony. The satellite colony established in 1971, however, began nesting in late June and I presumed therefore that these were mostly renesting attempts or first attempts by young birds.

Clutch size was 2.32 eggs/nest. Another central Alberta study (Fox, 1976) reported a mean clutch size of 2.11. Hebert (1985) reported a clutch size of 2.26 in a southern Manitoba colony. Erwin and Smith (1985) found the clutch size in 14 coastal mid-Atlantic colonies to vary from 1.67 to 2.74; in Quebec Chapdelaine et al. (1985) reported a clutch size of 2.50 from 295 nests; in New Jersey Burger and Lesser (1978) calculated a mean clutch size of 2.78 (2.55 - 2.89) in 34 colonies. There would, therefore, appear to be a tendency towards larger clutch sizes in the eastern population of common terns.

At Chip Lake, the percentage of one-egg clutches was 11.1%, of two-egg clutches 45.6%, and of three-egg clutches 43.3%. In Quebec, Chapdelaine et al. (1985) report 8.5%, 33.2%, and 58.3% respectively.

Incubation at Chip Lake was found to vary from 21-25 days, which is normal for the species (Palmer, 1941).

With regard to breeding chronology, nesting, and clutch size, I have therefore concluded that the Chip Lake common terns were typical. There is, however, some indication that the western population of common terns lay somewhat smaller clutches and that onset of nesting occurs earlier than nesting at similar latitudes in the eastern population. Confirmation of this suggestion, however, requires further study.

REPRODUCTIVE SUCCESS

Reproductive success (number of young fledged per nest) in common terns is well documented and has been found to vary from 0 to near 100% in the same colony from year to year and to similarly vary between geographically adjacent colonies in the same year. Erwin and Smith (1985) report reproductive success from 14 mid-Atlantic coastal colonies which varied from 0-1.83. In Massachusetts, Nisbet and Drury (1972) report a mean reproductive success of 0.92 (0.0-2.1) from six colonies. In another Massachusetts study, Nisbet (1972) reports a mean reproductive success in eight colonies of 0.40 (0.0-1.8). Chapdelaine et al. (1985) found productivity in a St. Lawrence River, Quebec, colony to be 1.24. In the lower Great Lakes, Morris et al. (1976) found reproductive success to vary from 0.07 to 0.9. In Alberta, Fox (1976) reported that reproductive success was 0.58 from a single colony. A two-year Manitoba study (Hebert, 1985) found reproductive success to be zero in one year and near zero in the next.

Factors which influence reproductive success are flooding, predation, habitat destruction, competition with gulls for nesting space, human disturbance, vegetation succession, weather, and availability of food. One or more of these factors are mentioned by most authors as being important.

In the nineteenth century, eastern terns were decimated by feather hunters, although this practice ceased early in this century and common tern populations increased to peak sometime between 1920 and 1950 (Nisbet, 1973a). Since the 1950's, common terns have declined somewhat but are now considered to be more or less stable over most of their range (Nisbet, 1973a; Kress et al., 1983; Nieme et al., 1986).

The reproductive success necessary to maintaining stable common tern populations was calculated by Austin (1929), who estimated—based on 17,500 eggs laid in Cape Cod, Massachusetts colonies—that 42% must develop as fully fledged juveniles. (Palmer (1941) considered this figure to be exceptionally high, but he did not suggest to what extent.) Using a median clutch size of 2.3 (this study) and Austin's estimation, this requires that 0.96 fledglings per nest are necessary to maintain a stable population. If a mean clutch size of 2.9 (Burger and Lesser, 1978) is used, 1.2 fledglings per nest are necessary to maintain a stable population. Austin's estimate is supported by Nisbet (1973a) who calculates that 0.9 to 1.1 per pair are necessary to maintain a stable population, this estimate based on his long-term study of the ecology of Cape Cod common terns. Assuming that Nisbet's (1973a) estimate is correct, the annual reproductive success I observed (0.1, 0.6, 0.02, and 0.6 respectively), therefore, falls below that necessary to maintain a stable population.

Hatching Success

Fracturing of eggs accounted for 9% (5-12%) of total egg failure at Chip Lake. This is not unusual in common terns and is generally attributed to eggs being rolled against each other, against a rock, or being struck by the tarsi of the adults when they rise in alarm or when they engage in territorial disputes (Palmer, 1941; Nisbet and Welton, 1984). In a study of common terns on the lower Great Lakes, Morris et al. (1976) report that in four colonies egg fracture resulted in 7% to 40% of egg failure. In an Alberta study, Fox (1976) found that 4% of eggs were fractured.

Eggs which I considered to be non-viable represented 6% of the total eggs laid at Chip Lake. Palmer (1941) reports that in his Cape Cod study 6% of the eggs were sterile; and in a study of Arctic terns nesting on a New Brunswick island, 15-17% of eggs laid were non-viable (Pettingill, 1939).

Abandonment at Chip Lake was 7% and consistent with that reported in other studies. Hebert (1985) observes an abandonment rate of about 15% in a Manitoba common tern colony; Fox (1976) reports 6% in an Alberta colony.

Observed predation was not an important factor at Chip Lake and exceeded 1% one year only. I attribute this mainly to the ringbilled gulls or the California gulls nesting on the island.

Egg disappearance was the single most important cause of egg failure at Chip Lake, accounting for 32% (21-44) of the total eggs laid. Egg disappearance is not unusual in common terns. Hebert (1985) reports egg disappearance of 53% in a Manitoba colony. Chapdelaine et al. (1985) observe a rate of 4.7% and Morris et al. (1976) record egg disappearance of 18.1% to 57.1% in four Great Lakes colonies. Although some authors speculate that predation may be a factor in common tern egg disappearance, it has not been documented.

In this study, I have ruled out predation as the major cause of egg disappearance. The only diurnal predators near the tern colony were ringbilled or California gulls, and at all times the terns vigorously defended the colony from them. Moreover, Morris et al. (1976) report high levels of egg disappearance in four common tern colonies and rule out gulls as the probable cause. Great horned owls (Bubo virginianus) are known to prey on common terns (Hebert, 1985; Nisbet, 1975). In Manitoba, a colony of common terns declined over two years of study and the cause of this decline was attributed to great horned owls (Hebert, 1985). In a Massachusetts study, great horned owl predation was to the extent that it caused "night desertion" of a large common tern colony (Nisbet, 1975). In response to nocturnal predation, the adult terns abandoned this colony each night and as a consequence the incubation period was extended six days longer than normal. I did not observe great horned owls near the colony, and the incubation period was normal. Accordingly, I have ruled out this form of nocturnal predation as a factor in egg disappearance. There was no evidence of mammalian predation and therefore the causative factor(s) of egg disappearance were probably internal rather than external.

Palmer (1941) discusses internal factors which he describes as "direct and indirect damage which the birds do to each other and to their eggs and young." Pettingill (1939) found in an Arctic tern study that the greatest loss of eggs and young was due to internal factors. Fox (1976) also suggests that the egg disappearance he observed in common terns was due to the terns themselves and not to external factors.

In terns, aggressiveness increases with the diminishing size of the nesting territory occupied by a single pair (Palmer, 1941), although the extent of the impact of crowding on reproductive success is unknown (Erwin and Smith, 1985). There must, however, be an optimal distance between common tern nests, which on the one hand reduces risk from internal factors and on the other is close enough that the terns can see one another and respond as a unit to external threat. Palmer (1941) states that 17 in. (38 cm) between nests is near the lower limit of tolerance in this species. In a study of 34 common tern colonies in New Jersey, Burger and Lesser (1978) found that on island colonies the nearest neighbor distance varied from 85 to 485 cm.

The distance between nests at Chip Lake was much closer than any other reported in the literature. Here it was common to find several active nests with no more than 25-30 cm between them.

One of the important factors affecting reproductive success in common terns is displacement by gulls, and this has been noted by many authors (Nisbet, 1973a, 1973b; Kress et al., 1983; Shugart and Scharf, 1983; Hebert, 1985).

Gulls, because they nest earlier, pre-empt nesting space and thus later nesters such as terns are relegated to less suitable space on the colony site or are obligated to relocate to another colony site which may be even less suitable (Morris and Hunter, 1979).

It is generally held that common terns exhibit philopatry (Austin, 1949; Morris and Hunter, 1979), although in response to displacement they readily move if suitable nesting areas are available (Marples and Marples, 1934; Morris and Hunter, 1979). McNicholl (1975) states that tern site tenacity is strongly developed in highly stable habitats but that in unstable habitats group adherence assists in pioneering of new or alternate habitats. This is not a mutually exclusive concept since habitat availability fluctuates and allows colonization of new sites or recolonization of old sites.

On Pelican Island at Chip Lake, the only space not occupied by gulls when the terns arrived and began to nest was the strip of beach on the southeast corner of the island (Figure 1). Because there were no other suitable sites of sufficient size on Chip Lake, the terns were relegated to this site on the island and very close distances between nests resulted. The consequent increased opportunity for aggressive interaction between breeding adults could account for egg disappearance. If eggs are broken in the nest as a result of territorial dispute, it is possible that these would be carried away in the same manner as eggshells are carried away after hatching. I offer the foregoing as a hypothesis only, as no direct observations were ever made of the cause of egg disappearance. It is, however, a phenomenon observed in common terns in several other studies.

Besides egg disappearance, the only other major cause of egg failure was flooding, which caused complete failure of the colony in 1971 and which prevented re-nesting in 1972.

The extent that investigation influenced hatching success is unknown. The major influence could have been an increase in egg shell fracture as the terns rose in alarm upon approach, and it is well documented that eggshell fracture can occur in these circumstances. Eggshell fracture at Chip Lake, however, was within the range reported from other studies.

Fledging Success

Fledging success was definitely influenced by investigation (except in 1971). Chicks were attacked by adults from nearby nests when they tried to hide, vegetation probably prevented chicks from returning to their nests, and chicks which swam away from the colony sometimes could not return.

Accordingly, I did not calculate or categorize causes of chick mortality. In 1970 and 1972, fledging success was 0.6/nest. Taking into account the impact of disturbance, it is probable that fledging success would otherwise have been higher and within the lower range proposed by Nisbet (1973a)—that is 0.9 fledglings per nest. In 1969 and 1971, reproductive success would have fallen below maintenance levels regardless of the impact of investigation.

DDE AND EGGSHELL THICKNESS

Levels of DDE excreted into the egg are considered to be a reflection of the body burden in the female at the onset of laying. I concluded that the source of the DDE in the Chip Lake common terns arose mainly from accumulation in their wintering grounds (Switzer et al., 1973). I drew this conclusion on the basis of the following: the minnows I collected in 1969 and 1970 contained no detectable levels of DDE or PCB's, and the terns began to lay shortly after arrival on the breeding grounds and would not have had time to accumulate the levels of DDE or PCB's which I observed. Moreover, Austin (1953) hypothesized that the northwestern population of common terns overwinter on the Pacific coast from California to Peru. In view of Saskatchewan tern band returns from these areas (Huston, 1972) and a Chip Lake band return from El Salvador, it appears that this hypothesis is correct and therefore DDE was accumulated in these areas. Consequently, the significant reduction in DDE levels each year of the study was a reflection of decreased exposure in the wintering grounds. I also concluded in 1973 that levels of DDT and DDE in the environment were degraded more rapidly than was generally proposed (Switzer et al., 1973). Many other studies and surveys have now confirmed this observation (Anderson et al., 1975; Frank et al., 1978a, 1978b; Butler, 1973; Butler et al., 1978; Blus and Lamont, 1979; Pearce et al., 1979; Henny et al., 1984; Warner et al., 1984). In fact, almost every study or survey shows a decline, beginning in the mid-1960's and continuing into the 1980's; these declines have been substantial. For example, a survey conducted by Klass and Belisle (1977) reports that mean DDE levels dropped by 84-99% in selected fauna in a New Jersey salt marsh between 1967 and 1973 and called these "rather rapid decreases." Butler (1973), in another survey of selected fauna, reports a "clearly defined trend toward decreased levels of DDT residues beginning in 1969-1970" from 15 states and over 8 years. These declines were found in studies of several species of birds. For example, Johnston (1974) collected 319 song birds (ten species) for the period of 1964 to 1973 during their fall migration through Florida. There was a steady and significant decline in DDT and metabolites from around 18 ppm to 3 ppm (lipid weight) over this period. Johnston (1974) attributes this decline to decreased DDT use. In least terns (*Sterna antillarum*) a 50% decrease in DDE was recorded between 1972-1975 by Blus and Prouty (1979), in clapper rails (*Rallus longirostri*) a "sharp decline" in DDE was recorded by Klass *et al.* (1980), in brown pelicans by Blus *et al.* (1979), and in two species of mergansers by Haseltine *et al.* (1981). In Connecticut and Long Island ospreys, DDE declined five-fold from 1969 to 1976 (Spitzer *et al.*, 1978); and in a large bald eagle study in eastern Canada, Grier (1982) recorded declining DDE levels from 1966 to 1981. Fleming *et al.* (1983) state that with respect to environmental levels generally, organochlorines have "decreased dramatically" in the last decade. There are, however, exceptions. Boellstorff *et al.* (1985) report that DDE and PCB's did not decline in white pelicans at Klamath Basin, California (although eggshell thickness increased).

Accordingly, the decrease in DDE that I observed in the Chip Lake common terns must be considered as indicative of generally declining levels of DDE for the period of 1969-1972.

At the same time, therefore, if DDE was causing shell thinning, I should have observed an increase in shell thickness over the four years of the study if the observed levels of DDE influenced eggshell thickness. This was not the case, and shell thickness was unchanged over the term of my study. Samples of eggs collected each year were considered independently, and of the nine categories of eggs (four years' whole samples, two subcategories in 1969, and three subcategories in 1970), only two showed a statistically significant inverse correlation between levels of DDE and eggshell thickness: specifically the 1970 whole sample (r_s= -0.267, coefficient of determination=7%) and the 1970 control sample (r_s= -0.521, coefficient of determination=27%). In 1969, I compared fractured eggs to non-fractured eggs and there was no difference either between eggshell thickness or between levels of DDE. In 1970, I compared fractured eggs, non-viable eggs, and non-fractured eggs. DDE levels in these eggs were the same; however, the fractured eggs were significantly thinner than the non-fractured or non-viable eggs.

In 1969 and 1970, I compared DDE and eggshell thickness based on position of the egg in the clutch sequence. Custer et al. (1985) found that in three Rhode Island colonies the third egg had about 10-20% higher organochlorine content than the first. Nisbet and Reynolds (1984) report the same concentration factor in Massachusetts terns. In the Chip Lake terns, I found that in

1969 there was a significant increase in DDE secreted into the eggs over the clutch sequence but that eggshell thickness remained unchanged over the sequence. In 1970, both the levels of DDE and eggshell thickness remained constant over the clutch sequence.

In summary to this point: tern eggshell thickness remained unchanged over time, although levels of DDE steadily declined; DDE was unrelated to eggshell fracturing, although in one year fractured eggs were thinner than non-fractured eggs; in one year, DDE increased over the clutch sequence, although DDE and eggshell thickness were unrelated to the position of the egg in the clutch sequence; finally, only two statistically significant correlations were found, and the dependent variable (eggshell thickness) interacted with the independent variable (DDE) only 7% and 27% of the time.

Several authors have hypothesized that ecologically significant eggshell damage begins to occur when levels of DDE exceed 8 ppm or more (wet weight, measured in the egg) (Lincer, 1975; Enderson et al., 1982; Henny et al., 1985; Ohlendorf et al., 1988). Accordingly, I considered the entire four-year sample as a composite and compared eggshell thickness on the basis of 0, 2, 3, 8, and 16 ppm of DDE. I found that eggshells from eggs with 8 ppm or more were significantly thinner than eggs with less than 8 ppm.

I was unable to directly measure the thickness of pre-1946 common tern eggshells. I did, however, weigh a 39-egg sample of pre-1946 common tern eggs from Western Canada and found the mean weight of the 1970 Chip Lake tern eggshells to be 11% less than the pre-1946 eggshells. Given that weight and thickness are highly correlated, I have therefore calculated by direct ratio that the pre-1946 eggshells would have been approximately 203 µ thick. Fox (1976) measured three pre-1947 common tern eggshells and found them to be an average of 200 µ thick. Using my estimate of 203 µ, the Chip Lake eggs with 8 ppm or more of DDE and 170 µ or less in thickness were approximately 17% thinner than pre-DDT common tern eggshells.

At first glance, this would appear to support the 8 ppm thinning hypothesis. However, if this hypothesis is true—at least for common terns—there should have been an annual reduction in the number of eggs which were 170 µ or less, consistent with the annual reduction in eggs containing 8 ppm or more of DDE. Indeed, this should be the critical test. There was, in fact, a sevenfold reduction in eggs containing 8 ppm or more between 1969 and 1972, which was significant. The number of eggs of 170 µ or less remained constant over the four years of the study. Hence my analyses strongly suggest that the hypothesized relationship of DDE to eggshell thinning is coincidental and not a cause and effect in common terns.

Support for the DDE-induced reduction in avian reproductive success finds support from two sources, namely field studies and laboratory studies. The field studies are of two kinds: comparison of pre- and post-1946 eggshells, and ecological studies of a given species. The laboratory studies are also of two kinds: feeding experiments and studies of reproductive biochemistry. In what follows I have critically reviewed the key studies supportive of the DDE/eggshell theory within the context of my findings at Chip Lake.

The first of what I shall call the "comparative eggshell" studies was initiated in 1966 by Ratcliffe (1967a). Ratcliffe reports that peregrine falcon populations in Great Britain had begun to decline in the mid- to late 1950's, and these declines appeared to show a correlation with areas where DDT was being used. It was concluded that eggshell damage was the major causative factor in this decline (although acute toxicity to other species of raptors caused by other organochlorine insecticides was also implicated: Lockie et al., 1970; Newton and Bogan, 1978). Accordingly, Ratcliffe decided to compare eggshells from pre-1946 to post-1946. He measured peregrine eggshells (collected in Ireland and Britain) using a method he devised now called Ratcliffe's Index (R.I.). He found that an abrupt decrease in the mean R.I., of approximately 16%, had occurred between 1946 and 1947. This, he claims, coincided with the introduction of DDT and DDT was therefore implicated in the decline of peregrine falcons which occurred in the mid-1950's.

This ready correlation, however, presents several paradoxes. Prior to the onset of World War II, the British peregrine falcon population had, according to Ratcliffe (1980), apparently been more or less stable.* On July 1, 1940, the Secretary of State for Air gave the Destruction of Peregrine Falcons Order, 1940; during the next six years, about 600 adult and immature peregrines were shot and young birds and eggs were destroyed (Ratcliffe, 1980). The purpose of this destruction was to protect carrier pigeons used to carry military messages. This depredation was to the extent that Ferguson-Lees (1951) estimates that the post-war nesting population of English peregrines was reduced to about one-half of its pre-war level. Following the end of the war, the "peregrine was well on the way to restoring its former population level..." (Ratcliffe, 1980); this restoration continued until the mid-1950's when it reached 95% of its pre-war level. From this point, peregrine populations began to decline until 1962 when, at about half of the pre-war level, a recovery began. By 1979, about three-quarters of the pre-war breeding territories were occupied (Ratcliffe, 1980). The second recovery was attributed to a reduction in the use of DDT.

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* This assessment, however, may be somewhat optimistic. Bannerman (1956) provides a different assessment: "When reviewing the status of this and other birds of the British List some years ago, two well known ornithologists, W. B. Alexander and David Lack wrote that in the last hundred years the peregrine has undergone marked and widespread decrease, and observed that it is now extinct in many counties due to human persecution."

Ratcliffe (1980, Figure 8, p. 212) presents a scatter plot of 2,253 peregrine eggshells that he measured, representing eggs collected between 1845 and 1979. It is apparent that an abrupt decrease in the eggshell index took place in 1946-1947. It would also appear from this scatter plot that the reduction in the eggshell index remains constant until around 1960-1961 when a slight increase occurs.

These data, however, raise the obvious question. If DDE was causing reproductive failure through eggshell thinning, how could the British peregrine population be nearly restored to its former population level during the decade of maximum shell thinning? The wartime control caused great reduction in the breeding population, which was reduced in some areas by half. Post-war, the breeding population nearly recovered to pre-war levels, but fell off to end-of-war levels and once again recovered to near pre-war levels. All of this occurred in face of a suddenly reduced and constant degree of eggshell thinning. Ratcliffe has not answered this question, which was first posed by Robinson (1970). Robinson commented on this "apparent paradox" and pointed out that all shell thinning occurred between 1946 and 1947, but the population increased rapidly from 1946 until the mid-1950's.

Unfortunately, Ratcliffe (1958, 1960, 1967a, 1967b, 1970, 1980) has not statistically described his voluminous data nor performed statistical analyses. Rather he has presented most of his raw data in table or plot form, and it is not clear to what extent a relationship exists between DDE and eggshell thickness. The levels of DDE in the British peregrines are not known prior to 1963. After this time, chemical analyses were performed and these raw data are tabulated by Ratcliffe (1980, Table 23, pp. 399-404).

I have summarized these egg residue data in Table 11. DDE residues peak in 1965 and 1966 and thereafter decline to more or less level off around 4-5 ppm from 1969 to 1978. However, Ratcliffe reports that British peregrines began to recover from the claimed pesticide-caused crash in 1962, from which time reproductive success more or less steadily increased. In other words, reproductive success began to improve during the period of the highest recorded DDE residues. This contradiction is similar to the contradiction posed by the peregrine recovery which occurred after the War in spite of maximum eggshell reduction. Although there may be ecological explanations for these apparently paradoxical observations, none has been put forward.

Year (n)	$\bar{X}$ DDE	Range
1963 (9)	6.9	0.2-22.0
1964 (3)	9.6	6.0-12.0
1965 (5)	19.9	10.2-25.0
1966 (6)	16.3	3.6-28.0
1967 (11)	7.1	1.0-18.0
1968 (11)	10.2	0.1-33.0
1969 (11)	6.3	0.6-16.0
1970 (8)	3.9	3.0-5.0
1971 (10)	4.8	3.0-13.0
1972 (7)	3.8	0.8-6.0
1973 (13)	3.7	0.8-21.0
1974 (12)	5.7	0.4-19.1
1975 (18)	3.1	0.8-11.0
1976 (18)	3.5	0.2-7.1
1977 (17)	4.1	0.6-9.2
1978 (19)	4.2	0.1-10.2

TABLE 11 Mean DDE Levels in 178 Peregrine Falcon Egg Samples (Eggs from Same Clutch Averaged and Considered as a Single Sample) Collected in England, Scotland, and Wales, 1963-1978, After Ratcliffe (1980, Table 23)

Gunn (1972a) has also reviewed Ratcliffe's theory, pointing out that eggshell thinning began in 1946 in the peregrine populations and was complete before DDT was in major use in Great Britain (1948). In response to Gunn (1972a), Cooke (1973) states that DDT was dusted on homing pigeons in 1946 and 1947 to control ectoparasites; because the peregrine preys on these birds, the eggshell thinning reported in 1946 and 1947 was caused by this source of DDT. Ratcliffe (1970, 1980) also states that this caused the eggshell reduction he observed in 1946 and 1947. To address this question, Peakall et al. (1976) analyzed the DDE content in the membranes of British peregrine eggs collected during this period. Of 13 eggshell membranes analyzed, nine contained detectable residues of DDE. They interpolated from these membrane levels and estimated the levels of DDE which would have been in the egg contents; the arithmetic mean of this sample can be calculated to be 1.46 (0-4.2) ppm wet weight of DDE. They conclude that this was sufficient to cause the eggshell thinning observed between 1946 and 1947. If this is the case, however, subsequent agricultural use of DDT could have made no contribution to the eggshell reduction in British peregrines.

In North America, Anderson and Hickey (1972) tested Ratcliffe's hypothesis by comparing the pre- and post-1947 weight, thickness, and R.I. of the eggs of 25 species of North American predatory birds (20,654 pre-1947 eggshells, 3,004 post-1947 eggshells). These data were described on a regional basis and 166 comparisons were made. What were considered to be statistically significant decreases were found in 62% of the cases. Of the 25 species of birds which were examined, 9 showed shell thickness reductions of 20% or more. Anderson and Hickey (1972), however, point out that they found inconsistencies geographically and within species. For example, the double-crested cormorant showed little eggshell reduction in Southern California in 1949 or in Florida in 1953 and 1960, but in Ontario there was 27% eggshell reduction in 1959. In addition, many of the post-1947 sample sizes were small—frequently less than ten and often only a few—and these were statistically compared to very large pre-1947 sample sizes—often several hundred—using parametric statistical tests. Nevertheless, the analysis conducted by Anderson and Hickey (1972) seemed to support Ratcliffe's hypothesis. Although other eggshell comparative studies were done (Faber and Hickey, 1973; King et al., 1978), the Ratcliffe studies and the Anderson and Hickey study formed the cornerstone of the hypothesis that the introduction of DDT coincided with reduction in the thickness of eggshells of several species of predatory birds.

The comparative eggshell studies of Ratcliffe and Hickey and Anderson stimulated the initiation of ecological studies of a variety of species of birds. In North America, decreases were reported in one or more of the three eggshell parameters in the following species: the prairie falcon (Fyfe et al., 1969; Enderson and Burger, 1970; Fimrite et al., 1970), peregrine falcon (Cade et al., 1971), brown pelican (Risebrough et al., 1971; Blus, 1970; Blus et al., 1971, 1974), osprey (Hickey and Anderson, 1968), great blue heron (Vermeer and Reynolds, 1970), double-crested cormorant (Risebrough et al., 1970); many other species reportedly showed eggshell reductions as well. The extent of eggshell reduction varied greatly from species to species and within individual species from location to location. In addition, there were often differences within a single population depending on which eggshell measurement was used. Generally, however, the extent of eggshell thinning was in the region of 10% with a few species as high as 20% or more. The highest recorded eggshell thinning was reported in brown pelican populations nesting off the Southern California coast, where some females laid eggs without shells and 35% eggshell thinning was recorded (Blus et al., 1971). At the same time, the highest recorded mean levels of DDT/DDE were reported in this population, often as high as 1000 ppm (lipid weight) (Risebrough et al., 1971). The source of DDT in the pelicans did not arise, however, from agricultural use but from effluent from a DDT manufacturing plant—at that time the largest in the world—where as much as 100,000 tons/day of DDT-saturated water was released (Gunn, 1972a). DDT was apparently accumulated by the pelicans in a fashion not unlike the robin and woodcock examples cited earlier.

Many of the field studies also showed a statistically significant but weak negative correlation between DDE and the eggshell parameter measured, and these observations were therefore used to support the DDE-induced eggshell thinning hypothesis.

As I have pointed out, however, the distribution of DDE residues in these studies was virtually always non-gausian and the residues in the Chip Lake terns are generally typical, both with respect to distribution and DDE levels. As a consequence, the arithmetic mean residue level, if not accompanied by additional statistical description, can be misleading as an indication of DDE levels. The great blue heron data (Vermeer and Reynolds, 1970) that

I cited earlier is a case in point. In addition, these early correlation coefficients were calculated using Pearson's product moment correlation coefficient which is inappropriate for data which does not show a bivariate normal distribution. A more appropriate correlation coefficient to describe these data is a nonparametric test such as Spearman's rank order correlation coefficient which, given the skew of the independent variable, will result in a more valid but weaker correlation than r_{xy}. In one study of eastern and western brown pelicans (Blus et al., 1972), an inappropriate statistical method was used to show a correlation between log DDE and eggshell thickness. Blus et al. (1972) draw their conclusions from statistical analysis of egg residues and eggshells collected over two years from three populations and two subspecies of brown pelicans. In 1969, 70 eggs were collected from 12 colonies: ten eggs from one colony in California, 21 eggs from two colonies in South Carolina, and 39 eggs from nine colonies in Florida. In 1970, ten more eggs were collected from one South Carolina colony. The condition of these eggs when collected is not described. Eggs from the nine Florida colonies showed thickness reduction up to 13% when compared to the pre-1947 thickness. The eggs from the two South Carolina colonies showed a mean reduction of 17% and the ten eggs from California showed a mean reduction of 35%. The DDE residues in the Florida and South Carolina colonies were mostly around 1-2 ppm (wet weight) with only seven exceeding 5 ppm but not 10 ppm. The ten eggs from California evidently contained a mean level of 71 ppm, ranging from around 30 to 125 ppm of DDE (Blus et al., 1972, Figure 1). These data are then combined to form one bivariate population. As far as applying regression analysis or correlation to such a composite group, Walker and Lev (1958) have clearly established the limitations of such analyses then they state:

> Sometimes two groups with widely separated means are thrown together to form one bivariate distribution. The correlations obtained from a composite group of this sort are spurious and meaningless.... When the groups have different means on one or both variables, the effect of combining them may be to produce a correlation coefficient larger than the correlation in the separate groups ... or smaller, or even different in sign.

It follows that logarithmic conversion would be similarly invalid.

Blus et al. (1972) also state that analysis of covariance revealed no significant differences among slopes of the three populations and that variation in eggshell thickness may therefore be explained by a common regression. The regression slopes of each population may well be related; however, no evidence is presented to show they are related to the common regression which is necessary if the common regression is used to explain the variation in each population. Regardless, Blus et al. (1972) concluded that a logarithmic relationship between DDE and eggshell thickness explained reduction in eggshell thickness. This logarithmic relationship was subsequently used by many authors to explain the DDE/eggshell relationship (Lincer, 1975; Newton and Bogan, 1978).

There were other difficulties in many of the field studies. Other lipophilic compounds, specifically PCB's, were usually present, sometimes in greater amounts than DDE (Hays and Risebrough, 1972; Morris et al., 1976; King and Flikenger, 1977; Haseltine et al., 1981; Custer et al., 1983a, 1983b) and these were often correlated with the eggshell parameter under study. Dieldrin was also often present and in some cases its impact could not be separated from DDE's (Blus et al., 1974).

White and Cromartie (1977) studied hooded mergansers (*Lophodytes cucullatus*), red-breasted mergansers (*Mergas serrator*), and common mergansers (*M. merganser*) from several North American sites and found that when compared to pre-1947 eggshells, the mergansers laid eggs 8.3% to 17.7% thinner. To draw this conclusion, sample sizes of as small as one or two eggs from the post-DDT era were used. They also found that PCB's were statistically correlated with eggshell thickness in hooded mergansers (r_s= -0.63) but that DDE was not. DDE and PCB's were, however, statistically correlated and White and Cromartie conclude that red-breasted and common mergansers contain potentially "dangerous levels of DDE." In another merganser study, Haseltine et al. (1981) found that in common mergansers shell thickness was only 2.2 to 3.2% less than pre-1947 and conclude, based on White and Cromartie's (1977) study, that an improvement of 14-15% in eggshell thickness had occurred in their common mergansers and this "substantial increase [was] primarily due to decrease in DDE." They drew this conclusion in spite of observing a statistical correlation of r_s= -0.029 between DDE and eggshell thickness and from eggs which contained three times more PCB's than DDE.

With respect to the DDE/PCB correlation mentioned above, the reverse logic is used by Newton and Bogan (1974). In a study of British sparrow hawks whose eggs contained 7.4 ppm (wet weight) of DDE, Newton and Bogan (1974) found a correlation between DDE and eggshell thickness (r=-0.359, P<0.001) and a correlation between PCB's and eggshell thickness ($r= -0.231$, $P<0.01$). However, because DDE and PCB's were correlated ($r=0.480$, $P<0.001$), Newton and Bogan (1974) therefore concluded that PCB's played no role in the observed shell thinning.

In an analysis of 47 peregrine eggs from the Rocky Mountain region, Enderson et al. (1982) found that eggshells were reduced by 16% but that only heptachlor epoxide showed a weak inverse correlation with shell thickness. A log plot of DDE "showed no apparent inverse relationship [$r_{xy}= -0.068$] contrary to expectation." The authors explain this observation by stating that DDE contamination was so uniformly high that a regression could not be shown. Yet DDE in these eggs showed a range of 8.3-65 ppm (wet weight x=23.3 and G.M.=19.6). They conclude that the eggshell reduction was caused by DDE by interpolating from Blus et al. (1972), discussed above.

In an Atlantic coast study of common terns, Custer et al. (1983a) analyzed 178 eggs from nine colonies and found low levels of DDE (geometric mean levels per colony never exceeding 0.78 ppm). PCB's, however, were much higher (geometric mean levels varied from 0.72 to 8.23 ppm in the nine colonies) and exceeded DDE by as much as 12 times in one colony. There was no statistical relationship between DDE and shell thickness, but there was between PCB's and shell thickness. Custer et al. (1983a), however, dismiss this relationship because "the r value was low (-0.221) and only 4.9% of the variance" could be explained by PCB's. Yet in this same report, Custer et al. (1983a) cite Switzer et al. (1973) as evidence of DDE-induced eggshell thinning where an r_s value of -0.269 is reported.

In an osprey study (Spitzer et al., 1977), 47 eggs were analyzed and the authors state that "the best correlation was with DDE." They also use r_s and confirm my statistical argument in this matter. Yet their conclusion is not supported by their own data. In only one of two DDE samples did a significant correlation exist (r_s= -0.70, n=13); in the other, it did not (r_s= -0.59, n=47). In addition, endrin was significantly correlated (r_s= -0.68, n=23) and PCB's, dieldrin, and mercury all showed correlations as well.

In another case, the results of an osprey study in Connecticut and Long Island is reported by Spitzer et al. (1978). This study showed that DDE residues had declined five-fold between 1969 and 1976 and that there had been no statistically significant increase in shell thickness. They state that "The cause of low productivity could not therefore be associated with certainty with any particular pollutant or with shell thinning per se." They also suggest that dieldrin may have affected productivity. The foregoing notwithstanding, the title of the article is "Productivity of ospreys in Connecticut-Long Island increases as DDE residues decline." In a double-crested cormorant study (Kury, 1969), DDE residues were greater than those in declining osprey populations and Kury states the "osprey is either unusually sensitive to pesticide residues or some other factor is causing its decline."

In a bald eagle study (Wiemeyer et al., 1984), 126 eggs were analyzed from 14 states, with emphasis on 1974-1979. The authors state that contaminants were highly intercorrelated and "This degree of intercorrelation made it difficult to determine which contaminants had an adverse effect on thickness and reproductive success." Indeed, of 14 organochlorines and mercury which were found in the eggs, only two did not show a negative correlation.

Some of the field studies presented other confounding data. For example, in a bald eagle study (Wiemeyer et al., 1972) of 23 eggs analyzed from Alaska (two sample groups), Minnesota, Maine, and Florida, mean DDE increased from 1.92, 2.91, 9.57, 14.95, and 18.37 ppm wet weight by state respectively (undoubtedly in consonance with DDT use) yet eggshell thickness was unchanged from state to state in all cases—10-11% thinner than pre-1947 eggshells.

Another example was another osprey study conducted in 1968 and 1969 (Wiemeyer et al., 1975) where 39 eggs were exchanged between Connecticut osprey nests, where DDE levels were high, and Maryland osprey nests where DDE levels were low. The Maryland osprey eggs transferred to Connecticut osprey nests hatched at a somewhat higher rate than the Connecticut osprey eggs transferred to Maryland nests, but the difference was not significant. The authors suggest that several factors besides DDE (although they do not demonstrate this) were involved in the "catastrophic" osprey decline, such as adult mortality and hurricanes.

in other field studies, the conclusions drawn were contradicted by the data of the studies. In a large 1966-1981 study of bald eagles nesting in northwestern Ontario, Grier (1982) calculates reproductive success based on the number of young raised annually to a late nesting stage from as many as 132 breeding areas. He found that reproductive success declined steadily from the highest level he observed in 1966 to the lowest in 1974; it then increased until 1981 (although never reaching the 1966 high). He also analyzed 19 addled eggs from 8 years of his study and states that they provide a "valid glimpse" of DDE residue levels in the bald eagle. What his own analyses show is a steady decline in DDE levels from 1968 to 1981, falling from a maximum of around 30 ppm wet weight in 1968 to around 5 ppm wet weight in 1981. Virtually every monitoring and ecological study which has evaluated DDT/DDE levels over the same time frame show the same reduction and most of these data were published by 1982. Nevertheless, Grier (1982) calculates the slope of the decline in eagle productivity from 1966 to 1974 and compares it with the slope of the improvement in eagle productivity from 1974 to 1981. He finds that they are significantly different and concludes that the 1972 ban on DDT was responsible for the improvement. His own data show that the highest eagle productivity was coincidental with the highest DDE residues; his data also clearly show that productivity falls in step with decreasing DDE residues. Finally, DDT use in North America peaked around 1958 and ceased in 1970, not 1972.

Nevertheless, Grier (1982) states, "These results confirm the suspected negative relation between DDE and bald eagle reproduction..." and "The rapid recovery of eagle reproduction since the ban on DDT is puzzling. DDE contamination in the environment and organisms at the site of the original application is known to remain for a long time."

Grier's (1982) study is cited by others as an example of DDE-induced reproductive failure. Wiemeyer et al. (1984), for example, state, "Grier (1982) found a significant inverse relationship between DDE levels in addled eggs and bald eagle reproduction in northwestern Ontario." They use this to support their inconclusive data as support for the implication of DDE in eggshell thinning in bald eagles, a study I cited earlier.

Another example of flawed reasoning is the conclusion drawn from a 1972 common tern study in Alberta (Fox, 1976). This population was studied for a single year and reproductive success was found to be below population maintenance levels. Although the literature conclusively confirms that common tern populations normally exhibit wide annual fluctuations, Fox (1976) opined that this population was failing. He also analyzed 13 fresh eggs as a control and found a mean DDE level of 3.98 ppm (0.05-11.08). A pooled sample of five dented eggs was analyzed and this single analysis yielded 6.67 ppm. Fox (1976) considered this to be a mean level, compared the means, and concluded that DDE caused eggshell fracture which explains the reason for the population failure. First of all, one year's assessment is inadequate to predict population failure, and a single analysis falling within the range of the control sample cannot be considered as different from the control. Moreover the degree of eggshell fracture he observed (4%) is normal for the species. This study is frequently cited as an example of a failing population, caused by DDE, of common terns (Findholt, 1984; Newton et al., 1986).

The field studies I have discussed are not atypical. Many, if not most, of the published egg measurement and ecological studies relating low environmental levels of DDE to reproductive failure in birds suffer similarly. Sample size is often a problem. It is not valid, for example, to compare three or four post-DDT eggshells, collected because they failed, with several hundred pre-DDT eggshells collected by oologists and to conclude statistically significant differences based on a parametric statistical analysis. For example, Faber and Hickey (1973) compared the eggshell thickness of 20 species of fish-eating birds using very small post-1947 sample sizes. In this study, three eggshells of the red-necked grebe (Podiceps grisegena) are compared with 112 eggshells from the pre-1947 era and found to be statistically significantly thinner ($P<0.00$). In the great blue heron, five eggs are compared to 228 and statistical significance is reported. The percentage decrease and the mean organochlorines in these 20 species are then plotted on a log basis and a linear relationship is concluded. Wiemeyer et al. (1978) use the same technique in an osprey study with sample sizes as small as two. There are also frequent problems with statistical description or analysis. Bivariate arithmetic means are used to compare different species when the distributions are clearly biased by a few highly contaminated eggs. Regarding statistical analysis, parametric techniques are often employed when non-parametric tests are called for. Statistical interpretations were made of questionable validity and with extremely small sample sizes. In one such instance (Blus et al., 1972), the conclusions drawn from such application form the basis upon which it has been concluded that a logarithmic relationship exists between DDE levels and eggshell thickness. The presence of other lipophilic compounds was almost invariably reported, and often these showed as strong or stronger correlation with eggshell thickness than did DDE. Eggshell thickness was frequently the same in contaminated and uncontaminated populations. Finally, the data of some studies completely contraindicated the conclusions drawn, and other studies presented unexplained paradoxes which, on the surface at least, seemed illogical. This assessment of the DDE/eggshell hypothesis does not stand alone. Several other scientists have commented on the troubling aspects of it (Robinson, 1970; Gunn, 1972a, 1972b; Devlin, 1974).

Nevertheless, most of the comparative eggshell studies and the ecological studies seem to show a correlation between DDE and eggshell reduction and consequent reproductive failure. Correlation, however, does not demonstrate cause and effect. Accordingly, and at about the same time, laboratory studies were undertaken to provide cause and effect proof to support the field correlations.

With only a few exceptions, the laboratory studies undertaken to elucidate the hypothesized shell thinning action of DDE share two similarities: first, they tested species of birds phylogenetically unrelated to the wild species suspected of failing because of DDE; and second they tested exposure levels of DDT/DDE greatly in excess of known environmental exposure levels. With respect to experimental design regarding this matter, Hunter and Lowry (1956) comment:

> In general, rigorous proof that a drug acts by inhibiting a particular enzyme would require 1.) that the enzyme concerned is inhibited in the living intact tissue or cells, 2.) that the enzyme block will quantitatively explain the effects of the drug, and 3.) that the enzyme inhibition occurs with an amount of the drug no greater [authors' emphasis] than that necessary to produce drug action under consideration.

Indeed, Hunter and Lowry emphasize point 3 above:

> As a minimum it is then necessary to show ... that the drug inhibits the enzyme concerned in vitro at concentrations consonant with the dosages effective in vivo.

Lundholm (1987) has reviewed the literature respecting the mode of action of DDE and has "suggested as a working hypothesis" that the enzymatic effect(s) of DDE are on, or in, the mucosa of the shell gland. He derived this hypothesis after study of the literature and experimentation with two species of ducks, the Indian Runner duck and the Swedish-Rouen duck, which were exposed to 40 ppm of DDE.

Any animal exposed to sufficiently high levels of a toxicant will demonstrate evidence of changes in reproductive physiology. Not surprisingly, this is the case in most, although not all, DDT/DDE laboratory studies. I summarized some of these findings earlier. It is, on the other hand, also not surprising that the mode of action of DDE on some aspect of reproductive physiology has not been elucidated beyond a suggested working hypothesis, since DDT's basic mode of action is unknown.

Exposure levels of wild birds to DDE has been reasonably well documented. For example, Lincer and Sherburne (1974) studied the exposure level of wild kestrels in the eastern United States and found that items in the diet rarely exceeded 0.01 ppm. Enderson and Burger (1968), Cade et al., 1968, and Enderson et al. (1982) measured the organochlorine residues in pooled prey species of peregrine falcons from Northern Canada and the Rocky Mountain region of the United States in the late 1960's and early 1970's and reported levels rarely exceeding and generally much less than 0.9 ppm of DDE. In other studies, the concentration factor of prey to adult has been calculated and it is about 15-30 times (Enderson et al., 1982). Accordingly, one can make a rough estimate of exposure levels generally to a population of birds, although not to an individual. During peak years of DDT use, this level would rarely have exceeded 1 ppm and this exposure level would have declined as environmental levels of DDT declined.

The laboratory studies, then, which should be the landmark test of the DDE/eggshell hypothesis, should be those studies which approximated environmental levels and which tested species phylogenetically related to the wild species which were declining. Two research programs have been conducted which come closest to meeting these criteria.

These two programs both exposed domestically raised kestrels to low levels of DDE. The kestrel is a small falcon, congeneric with the peregrine falcon; since the peregrine is considered to be one of the most, if not the most, sensitive birds to DDE, kestrel studies using low levels of DDE should provide the most valid evidence of a cause and effect link. Porter and Wiemeyer (1969) exposed two groups of domestically raised kestrels to 1 ppm dieldrin plus 5 ppm DDE, and 3 ppm dieldrin plus 15 ppm DDE (wet weight) respectively for two years. In both years of the study, the control group laid eggs which were 7% and 11% thinner than pre-1947 kestrel eggs (Anderson and Hickey, 1972; n=1,251, $\bar{x}$=211 μ). The dosed groups laid thinner eggs than the control group, but there was little difference between the low dose group and the high dose group. With respect to this study, Robinson (1970) states, "[there are a] number of conclusions ... some of which appear to be of doubtful validity." In a follow-up study, Wiemeyer and Porter (1970) exposed domestic kestrels to 2.8 ppm DDE (wet weight) for two years and compared eggshell thickness between this group and a control group. In the first year of the study, the control group laid eggs measuring 188 μ (130-210); in the second year of the study, 184 μ (130-210). In the first year of the study, the experimental group laid eggs that were 186 μ (165-203) and in the second year laid eggs that were 168 μ (153-185). The mean DDE egg levels in each year of the study were 3.09 (1.05-5.89) and 32.4 (17.4-44.2) ppm wet weight respectively. The authors conclude from these data that "DDE induced thinning of kestrel eggshells in a controlled experiment further strengthens the hypothesis ... of thinning in wild ... birds." The data from this study raise several questions, but one in particular. In both years the control population laid the thinnest shelled eggs. Assuming that the range of eggshell thickness of the eggs laid by the controls is normal for the species, then both dosed groups are well within that range. In fact, the thinnest eggs laid in the dosed group were 22% and 16% thicker respectively than the thinnest eggs laid each year by the control group.

Lincer (1975) also domesticized kestrels for laboratory feeding experiments. These kestrels were captured along the New York coast during the autumn of 1970. They were kept in captivity on a DDE-free diet until mid-March, 1971, when they were divided into groups and exposed to 0.3 ppm (2 pairs), 3.0 ppm (5 pairs), 6.0 ppm (2 pairs), and 10 ppm (2 pairs) DDE for five and one-half months. The control group consisted of four pairs and laid 15 eggs which were reduced by 13% (R.I.) when compared to pre-1947 eggs. On a thickness basis they were fully 19% thinner. The 0.3 ppm exposure group laid 8 eggs which were reduced by 6.0% (R.I.) and showed 9% thinning. The 3.0, 6.0, and 10.0 ppm feeding groups showed shell reduction of 25.5, 28, and 32% (R.I.) respectively. Residue levels in each group were 0, 7.8, 85, 154, and 245 ppm (dry weight).

In a parallel study, Lincer and Sherburne (1974) analyzed 39 wild kestrel eggs over the same four years as Lincer's (1975) feeding study and found them to contain 37.7 ppm DDE (dry weight) and to be 10% thinner than pre-1947 kestrel eggs. (In one year of this study, PCB's were analyzed and these were found to be nearly equivalent to DDE.) In other words, the DDE-free control group of experimental kestrels laid eggshells 19% thinner than pre-1947 kestrel eggshells, yet wild kestrels of the same stock, analyzed over the same time frame and containing residues of 37.7 ppm DDE, laid eggs only 10% thinner than pre-1947 kestrels. Moreover, the low-exposure group laid thicker eggs than the control group. Lincer (1975) explains that "all of the experimental birds laid thinner-shelled eggs, which might be attributable to genetic differences and/or to effects uniquely associated with captivity." In Figure 4 of Lincer (1975), bivariate means of DDE content of eggs and percentage decrease in eggshell thickness of several North American raptors from separate studies are plotted on a log basis. Only two of the 12 species plotted show more shell thinning than the control group of his study.

Lincer (1975) nevertheless concludes, "There can be little doubt now as to the causal relationship between the global contaminant DDE and the observed eggshell thinning and consequent population declines in several birds of prey."

The Wiemeyer and Porter (1970) and Lincer (1975) studies are probably the most frequently cited laboratory studies of "proof" of a causal relationship between DDE and eggshell thickness. Contrary to the conclusions made by the authors of these studies, the results show a stronger indication, on the face of it, that DDE at low levels causes eggshell thickening and not eggshell thinning.

At Chip Lake, I found an 11% mean reduction in eggshell weight from pre-1947 eggshells, which was not related to levels of DDE (which declined from 7.57 ppm to 2.98 ppm, wet weight, over the four-year study). I have noted the non-gausian distribution of the DDE residues in the Chip Lake terns, and this same distribution characterizes virtually all studied wild bird populations.

It is well known that a wide variety of factors normally induce eggshell thinning in a population of birds (Anderson and Hickey, 1970; White and Cromartie, 1977). These factors include age, pathology, injury, parasites, availability of food, and weather. It is entirely reasonable that these extrinsic and intrinsic factors would not operate uniformly in a population of birds and accordingly, a few birds will lay thin-shelled eggs in any given season. It is also highly likely that the stressors which lead to thin eggshells will also result in drain on lipid reserves, thereby concentrating organochlorines in the reduced lipid tissue fraction. Consequently, when lipid is mobilized for egg laying, those members of the population with more concentrated chlorinated hydrocarbons will deposit more in their eggs than those members of the same population who are not suffering these natural stressors.

This may well be a more plausible explanation of the DDE/eggshell correlation in many species than the cause and effect relationship that so many authors suggest.

The degree of eggshell reduction reported in most studies is based on a comparison of eggs collected by oologists or by museum collectors prior to 1947 with eggs collected by ecologists after 1947. The pre-1947 eggs would definitely not reflect thinner-shelled eggs or eggs which had failed for other reasons. It is also not unreasonable to assume that these collections would somewhat favor thicker eggs laid by the populations from which they were collected. When this kind of sample is compared with a much smaller sample of eggs, collected from a single population because they had failed, or a random sample from a single population, it is logical to presume that there would be a reduction in the mean parameter being measured in the post-1947 sample. Moreover, when a large sample with a small variance is compared with a small sample with a large variance using powerful parametric statistical applications, the validity of the results of such an application are doubtful (Montgomery, 1984; Miller, 1986).

The avian population declines reported in the literature also bear scrutiny. With respect to the peregrine falcon, Hickey (1942) reports that the American population east of the Rocky Mountains and excluding Alaska had been declining by 10% per decade since the turn of the century. This represented a 50% reduction until, by 1942, there were about 140 nesting pairs (Consolidated DDT Hearings, 1972b) in the eastern United States. This decline was attributed to a variety of factors, with habitat destruction and shooting being important.

Enderson and Berger (1968) studied peregrines in northern Canada during a period of great DDT use in North America and found "that their eggs bear about twice the levels found in eggs from the stricken British Peregrine population, and even with these precariously high levels the Canadian Peregrines appear to be reproducing normally." Cade et al. (1968) also studied Alaska and Yukon peregrines during the period of great DDT use and state,

> But how does one explain the association of high residue levels in these Peregrines with an undiminished population and unhampered reproduction? Either the hypothesis that the decline in Peregrine populations elsewhere has resulted from the organochlorine residues is incorrect, or else these Yukon Peregrines must be precariously poised near some threshold level that will prove inimical once reached.

Mean DDE egg levels which were recorded in these two studies were 27.1 ppm wet weight and 15.0 ppm wet weight.

A management plan to re-introduce peregrines in areas in North America where they were reduced or eliminated was undertaken and, by 1978, 133 domestically raised birds had been released (Anon, 1978). Approximately 300 peregrines are now annually released in North America (Shelford, 1988). The success of this program is apparently unknown.

I mention the foregoing because in many cases where population recoveries have occurred, attributed to reduced levels of DDT, there are also management and protection programs which were put in place at about the same time.

In the case of the osprey, for example, improvement in reproduction began in the late 1960's, attributed to a reduction in DDE (Spitzer et al., 1978). Henny et al. (1977) report that programs such as establishment of management zones and erection of nesting platforms have also been important. Indeed, only 26% of the ospreys nesting in Chesapeake Bay by the early 1970's utilized trees; the remainder nested on nesting platforms or other man-made structures (Henny et al., 1977), many of which were erected for that very purpose.

Caspian terns (Sterna caspia) are another example in point. These birds have increased by 60% since 1960 on the west coast of North America. They nest in relatively contaminated areas such as San Francisco Bay, making use of man-made structures (Gill and Mewaldt, 1983).

Vermeer and Sealy (1984) report that double-crested and pelagic cormorants (Phalacrocorax pelagicus) have been increasing on the west coast of Canada since the 1920's, and the increase has been more rapid recently. They attribute this to termination of "egging."

Jehl (1984) reports that the problems facing sea birds in the Pacific Northwest and California relate to human disturbance and that gill netting is a serious problem. In fact in a single year, of 22,000 sea birds washed ashore in Monterey Bay, 90% drowned in gill nets (Jehl, 1984).

Hatch (1983) found that Massachusetts populations of double-crested cormorants have been doubling every 3 to 4 years since 1974, and he attributes this to expanding populations of fish which cormorants prey upon. Price and Weseloh (1986) also report expanding cormorant populations on Lake Ontario. They state that past declines were due to fishermen who shot adults, smashed eggs, and to mortality caused by nets. They attribute the increase to protection and immigration.

I have cited the foregoing examples to illustrate that the factors affecting bird populations—and large predators in particular—are extremely complex. Simple, straight-line correlations, based on small sample sizes, anecdotal information, and only suggested working hypotheses derived from unrelated species exposed to high levels of DDE and invalid statistical application, should not be construed as cause and effect proof, particularly when other factors may have played as important or more important a role in observed population declines or increases.

VII. CONCLUSION

Common terns nesting in central Alberta in 1969-1972 arrived on their breeding grounds carrying DDE, most of which must have been accumulated on their wintering grounds along the Pacific coast of California, Central America, and northern South America. The levels of DDE significantly declined each year of my study, a reflection of decreasing use of DDT. The shells of eggs laid by the Chip Lake common terns were reduced in thickness by about 11% when compared to pre-1947 eggshells. Although levels of DDE decreased each year of the study, eggshell thickness remained constant over the four-year study period. There was indication that DDE increased over the clutch sequence but that shell thickness was unaffected by such increase. There was also indication that thin-shelled eggs were more readily fractured than thicker-shelled eggs but that levels of DDE were unrelated to eggshell fracture.

I found that in the entire sample of 300 eggs, eggs containing more than 8 ppm also had eggshells which were significantly thinner than eggs containing less than 8 ppm. This association, however, was probably coincidental and not demonstrative of cause and effect. Eggs containing 8 ppm and more of DDE significantly declined over the term of the study; the number of thin eggs laid each year of the study remained constant.

I have therefore concluded that the levels of DDE carried by this population of common terns was unrelated to eggshell thickness and thus unrelated to reproductive success. I have also hypothesized that natural external and internal stressors led to production of thinner eggs, and that these same factors led to concentration of DDE in the lipid tissue which was subsequently mobilized and reflected in the egg DDE levels.

Reproductive success was impacted by my intrusion into the colony. I have calculated, however, that reproductive success would otherwise have been within the normal range for two of the four years in the absence of my activities.

Egg disappearance was the most important natural factor in reproductive failure. I attributed this to intrinsic factors in the tern population which were indirectly related to displacement by the two species of gulls occupying the island. The other major factor influencing reproductive success was flooding, and this too was related to displacement by the gulls. All of the major factors influencing reproductive success have been reported for other populations of terns. The extent of egg fracturing, egg infertility, and egg abandonment that I observed were normal for the species.

I have accepted, therefore, the null hypothesis of my study: that is, DDT and its principle avian metabolite DDE do not influence reproductive success through reduction of the eggshell in common terns at the levels of DDE observed from 1969-1972.

My review of the literature within the context of my findings strongly suggests that the ready correlation between DDE, some eggshell parameter, and reproductive failure has been greatly over-simplified. The suspected mode of action of DDE on the shell gland has not been elucidated beyond a suggested working hypothesis—in spite of 20 years of research. Moreover, this hypothesis is developed largely with species phylogenetically remote from the species apparently failing because of DDE and employing levels of DDE greatly exceeding environmental levels. The controlled feeding studies with species most congeneric with apparently failing wild species do not show that low levels of DDE cause eggshell reduction. The ecological studies which have purported to show DDE-induced reproductive failure through eggshell thinning present contradictions and unexplained paradoxes. Many of them present data which contradict the conclusions drawn. Finally, many of these field studies report data which were analyzed by statistical tests which are inappropriate, both from the perspective of sample size and from the perspective of the assumptions which underlie the appropriate application of these techniques.

I am of the assessment that natural factors more readily explain observed eggshell reduction than does DDE in those species of birds which show only a few highly contaminated eggs. Almost without exception, where species of birds show population declines, there is evidence of land use change and practices, habitat destruction, and human interference and depredations. Where populations are recovering from declines, protection and management programs are often a factor.

In conclusion, I believe that a combination of intrinsic and extrinsic factors explain many of the reported DDE-eggshell relationships and that in several species it is coincidental to these factors. I also believe that in many species this reported relationship is a function of the manner in which the data have been interpreted rather than demonstration of a cause and effect relationship.

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APPENDIX 1

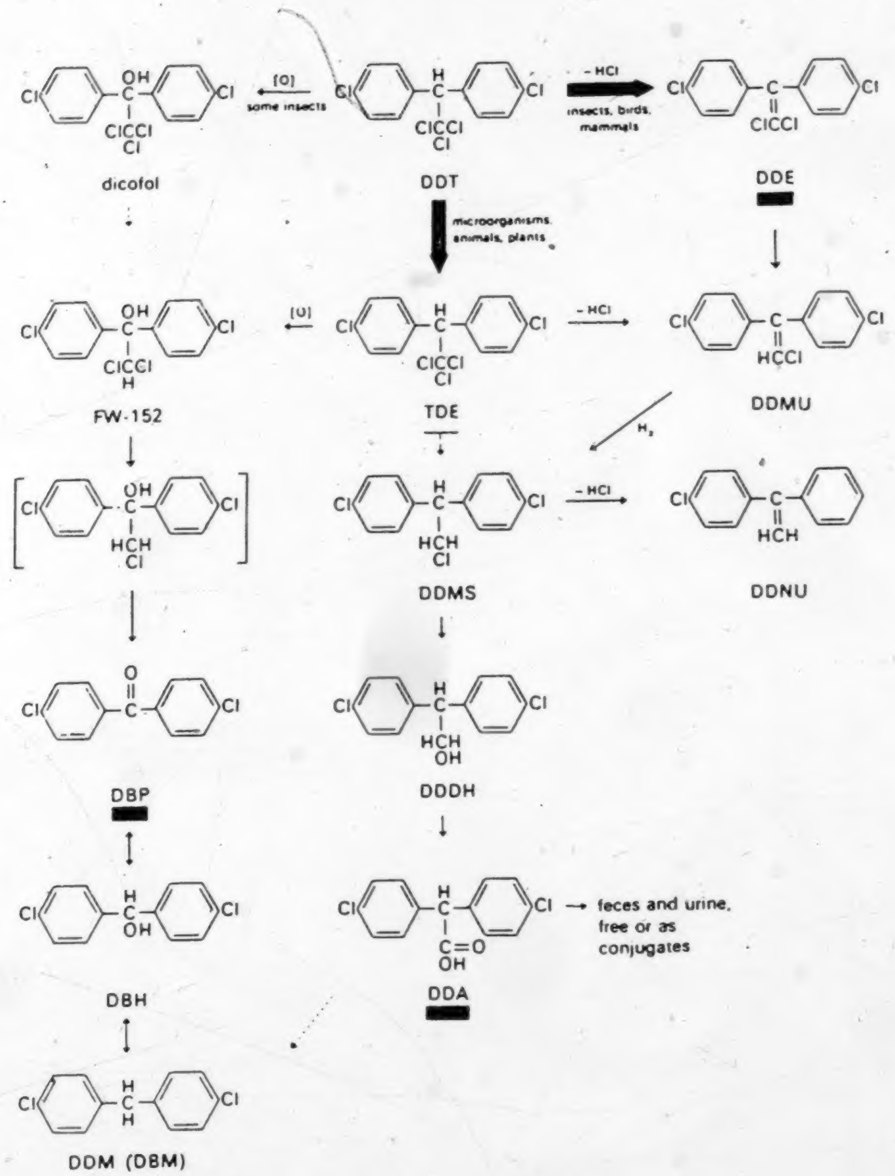
Chemical Names of DDT and Metabolites Discussed in the Text

DDT	1,1-trichloro-2,2-bis(chlorophenyl) ethane
DDE	1,1-dichloro-2,2-bis(chlorophenyl) ethylene
DDD	1,1-dichloro-2,2-bis(chlorophenyl) ethane
DDA	2,2-bis(chlorophenyl) acetic acid
Kelthane	4,4 dichloro-α-(trichloromethyl) benzhydrol

APPENDIX 2

Chemical Structure and Metabolic Conversion of DDT in Plants and Animals (After Matsumura, 1975)

dicofol = kelthane
TDE = DDD


dicofol
[O]
some insects
DDT
– HCl
insects, birds, mammals
DDE
microorganisms, animals, plants
FW-152
[O]
TDE
– HCl
DDMU
H_2
DDMS
– HCl
DDNU
DBP
DDDH
DBH
DDA
→ feces and urine, free or as conjugates
DDM (DBM)